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No. 141.

POLYDACTYLISM IN MAN AND THE DOMESTIC ANIMALS, WITH ESPECIAL REFERENCE TO DIGITAL VARIATIONS IN SWINE.

BY C. W. PRENTISS.

WITH TWENTY-TWO PLATES AND TWENTY-SIX TEXT FIGURES.

FROM THE BULLETIN OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE, VOL. XL. No. 6.

CAMBRIDGE, MASS., U. S. A.
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Polydactylism in Man and the Domestic Animals, with especial Reference to Digital Variations in Swine.

By C. W. Prentiss.

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Introduction.

The frequent occurrence of extra digits on the extremities of both man and the domestic animals has attracted the attention of many anatomists during the past century. Various theories have been advanced to account for the appearance of these digital abnormalities, and the opinions expressed by different investigators have been remarkably contradictory.

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Through the great kindness of Dr. W. McM. Woodworth, Keeper of the Museum of Comparative Zoölogy at Harvard College, a valuable collection of polydactyle specimens was placed at my disposal. The investigation represented by this paper was undertaken with the view to obtaining, from a study of these abnormalities, some clue as to the causes leading to their occurrence.

In order to understand the phenomena of polydactylism, and to make it possible to draw some general conclusions, a comparative study of such abnormal structures is necessary. It has, therefore, been considered worth while to collate from the literature brief descriptions of polydactylism in those forms of which we were unable to obtain suitable material. In reviewing the literature, however, a résumé is given of only those papers which draw important and general conclusions. Works concerned chiefly with descriptions of polydactylism in individual animals are treated of in the separate accounts of digital variations in man and the different domestic animals here referred to.

My research was carried on at the Zoölogical Laboratory of Harvard University, and to Prof. E. L. Mark are due my sincerest thanks for both the laboratory privileges I enjoyed, and his own kind direction and most valuable criticism. To Dr. W. E. Castle I am also indebted for important criticisms and revision of proof.

I. Historical Survey.

Allusions to polydactylism are to be met with as far back as the time of Pliny. The first investigator who attempted to collect scientific data on the subject was Struthers (**'63**). He tabulated digital abnormalities in man, and proved that they were strongly inherited.

Darwin (**'76**) accounts for the fact that supernumerary digits are more numerous on the hands than on the feet by suggesting that the hand is more specialized than the foot, and therefore more likely to vary. For the same reason polydactylism is less common in women, the male showing always greater differentiation, and therefore a greater tendency to variation. Darwin at first assumed polydactylism to be reversion to a more primitive ancestral condition; but this assumption was later withdrawn.

Gegenbaur (**'80**) criticises the theory which regards polydactylism as atavistic. His arguments are: (1) that other parts of the manus or pes shew no correlated modifications; (2) that man normally possesses five digits, the typical number for vertebrates, and that the supernumerary digits are produced by duplication or intercalation. He regards all cases of polydactylism in the pig as due to the splitting of one of the functional digits, and holds therefore that they are monstrosities. Polydactylism in the horse, he admits, may be atavistic, as (1) the reversion is to a closely related ancestor; (2) in Hipparion, a three-toed fossil horse, the second digit is better developed than the fourth, and in polydactyle horses the second digit is the one which most usually appears; (3) the rudiments of the extra digits may be present in the embryo. Atavism Gegenbaur divides into two types: (1) Palaeogenetic, or cases where the fundament of an organ is always present in the embryo, and may develop, or may degenerate (centrale of man); (2) Neogenetic, or cases where the organ is absent even in the embryo, (phalanges of digits II and V in the horse).

Bardeleben (**'85, '85ª, '86**) answers Gegenbaur's objections to reversionary polydactylism in man, by advocating the prae-pollex theory. He maintains that the cartilaginous elements found on the radial side of the hand and the tibial side of the foot are rudiments of a "prae-pollex" and "prae-hallux," respectively, and not sesamoids, as had been previously maintained. Also that the pisiform of the carpus and the tuberositas calcanei of the tarsus represent the rudiments of "post-minimi." The manus and pes of primitive mammals were therefore in his opinion heptadactyle, and polydactylism in man and other mammals is simply reversion to this ancestral seven-toed condition.

Boas (**'85, '90**) considers polydactylism in the horse and ox as due to reversion. The extra digits formed do not represent simply the persistence of an embryonic condition, for in the polydactyle ox phalanges are formed in the extra digits, and these elements are normally absent in the embryo.

Albrecht (**'86**) points out that in man the greater number of polydactyle cases consist in the duplication of a single digit. This he assumes to be reversion to the bifid fin-rays of the elasmobranchs. He distinguishes this type of polydactylism (false hyperdactyly) from that found in animals where the number of digits is less than five (true hyperdactyly). Albrecht is supported in his view by Kollman (**'88**).

Gegenbaur (**'88**) states that the discovery of the so-called "prae-pollex" is not new, but was originally made by Cuvier, and he opposes the "prae-pollex" theory of Bardeleben on the following grounds: (1) these doubtful rudiments never form true fingers, and their development is secondary to that of the other digital bones; (2) polydactylism in man cannot be explained by it, for supernumerary digits occur on the ulnar as well as on the radial side of the carpus, and they may also be interpolated between the other digits; (3) when the "prae-pollex" is present, no correlated changes have been observed in the carpus and other parts of the manus; (4) its inheritability is no proof of reversion to a palingenetic digit, for all monstrosities are inherited. Bardeleben's theory is therefore an "unbegründete Behauptung," and polydactylism in man is due to doubling of the normal digits.

Zander (**'91**) describes in some detail a case of hexadactylism in man, concluding that the abnormality was produced by the splitting or duplication of the fundament of the normal thumb. He discusses at some length the different theories which have been advanced to account for polydactylism. Reversion and the assumption of Bardeleben he rejects on the following grounds: (1) the rudiments of the prae-pollex are of secondary formation, and therefore are sesamoids, not digital vestiges; (2) Kükenthal (**'89–93**) has shown that the sixth digit found in Delphinus leucas is produced by the splitting of the fifth digit in the embryo; (3) the most primitive fossil reptiles, the Ichthyopterygia, possessed, according to Baur (**'87**), only five digits, and therefore the hexadactyle condition must have been brought about later, either by duplication of the primary digits, or by neomorphic development on the ulnar side of the extremity; (4) no case has been observed where the "rudiments" of Bardeleben have developed into supernumerary digits. On the contrary, the extra fingers of man are usually attached distally, where no rudiments exist. Polydactylism in man, therefore, cannot be atavistic, but is due to duplication of normal digits. This duplication is caused *in utero* by the pressure of amniotic threads.

This explanation was first proposed by Ahlfeld (**'85–86**), who observed at the birth of an infant with a divided thumb that an amniotic thread was still present in the fissure of the duplicated digit. This theory accounts most satisfactorily for the different stages of division to be met with in cases of polydactylism and polymelia; for, the earlier the amnion presses upon an extremity of the embryo, the more complete and far-reaching will be the duplication produced.

Marsh (**'92**), in treating of polydactylism in the horse, gives little weight to the fact that the ungual phalanges of the supernumerary digits never revert to the partially cleft condition peculiar to the fossil horse. But he concludes (p. 351) that "All the examples of polydactylism in the horse which the writer has had opportunity to examine critically are best explained by atavism, and many of them admit of no other explanation. Taken together with their great frequency they clearly indicate the descent of the horse from comparatively recent polydactyle ancestry."

Blanc ('93) recognizes three distinct classes of polydactylism: (1) Atavistic, or cases where ancestral digits reappear; (2) Teratological, or cases in which either normal digits or atavistic supernumerary ones are duplicated; (3) Heterogenic, or cases belonging to neither (1) nor (2).

(1) *Atavistic polydactylism.* Bardeleben's theory is accepted without reservation. Atavism is regarded by Blanc not as the neo-generation of an ancestral digit, but merely as the development of rudiments normally present in the embryo. From an examination of digital abnormalities in mono-, di-, tetra-, and penta-dactylous animals he deduces the following general principles: (*a*) the more simple the extremity, the more varied and the more divergent from the normal are the forms of polydactyly. (*b*) In all species the thoracic limb presents ancestral digits more frequently than the pelvic does; this leads to the conclusion that the manus has become simplified later than the pes. (*c*) In man the postminimus appears more frequently than the prae-pollex or prae-hallux; the reverse is true for other animals.

(2) *Teratological Polydactylism.* The proximate cause of these abnormalities Blanc regards as obscure, but he favors Albrecht's ('86) view of reversion to the pterygian fin rays of selachians; the single digit of the higher animals represents two of these rays fused.

(3) *Heterogenic polydactylism.* This consists usually of the intercalation of extra digits, and the producing cause is unknown.

If Albrecht's view is accepted, Blanc proposes the following classification of polydactylism:

1. *Atavistic polydactylism.*
   - a. Reversion to the pentadactyle or mammalian type.
   - b. Reversion to the heptadactyle or reptilian type.
   - c. Reversion to forms possessing a double series of phalanges or to the selachian type.
2. *Heterogenic polydactylism.*
   The supernumerary digits are monstrosities.

Bateson ('94) studied polydactylism in the cat especially, but cites and figures a large number of digital variations in the other domestic animals and in man. His conclusions are: (1) Polydactylism occurs much more frequently in certain species than in others. (2) Particular forms of digital variation are peculiar to particular animals. (3) The abnormality usually occurs symmetrically placed on both sides of the body, and often on both fore and hind extremities. (4) There is a tendency for the abnormal digits to form systems of minor symmetry. (5) Polydactylism is due to variation, and not to reversion.

Wilson (**'96**) gives an account of five cases in man where polydactylism was transmitted through several generations, and concludes that the abnormalities are generally constant in position, but variable in degree. In reviewing the different theories advanced to account for polydactylism he rejects that of reversion and Bardeleben's prae-pollex theory on grounds similar to those put forward by Gegenbaur (**'80, '88**) and Zander (**'91**), and holds that germinal variation is the proximate cause.

If we summarize the conclusions of the various investigators whose work we have briefly reviewed, it appears that three explanations have been proposed to account for the occurrence of digital variation: (1) Reversion, or Atavism. (2) External stimuli (pressure of amnion *in utero*). (3) Internal stimuli (germinal variation). A discussion of these theories will be more in place after we have examined for ourselves the types of polydactylism occurring in the different domestic animals. In proceeding with this examination we must keep these three theories clearly in mind. If we are warranted in rejecting Bardeleben's prae-pollex theory, the possession of six digits by any domestic animal must be accounted for on grounds other than reversionary. And only in animals normally possessing fewer than five digits may we look for atavism to restore, either partially or completely, the typical number of digits; even in these cases the supernumerary parts may be produced by the duplication of one or more of the normal digits. Throughout the following pages, therefore, we shall endeavor to determine as definitely as possible the respective parts which these supposed causes play in producing polydactylous abnormalities.

The special point which we have to determine is whether the extra digits which appear in polydactylism are of palingenetic or neogenetic origin, — whether they are returns to old structures, or represent new variations. The term reversion has been loosely used to designate the general phenomenon of heredity. To avoid confusion I shall limit its meaning to the abnormal inheritance of *palingenetic* characters, while heredity will be used in the broader sense. Beginning with the typical pentadactyle extremity characteristic of man and the Carnivora, we shall take up in turn those forms in which the number of functional digits has been reduced (fowl, swine, Ruminantia, and Equidae).

II. Polydactylism in Man.

A. LITERATURE.

On account of its importance to the medical profession, polydactylism has been more often observed in man than in other vertebrates, numerous cases having been described. Unfortunately the majority of the descriptions are confined to the external appearance of the abnormalities, and to the structure of the skeletal parts; the anatomy of the muscles, and still more important, that of the nerves, has seldom been thoroughly worked out. Besides the many instances cited by Bateson (**'94**), the observations of Morand (**1773**), Förster (**'61**), Struthers (**'63^a**), Ahlfeld (**'85–86**), Fackenheim (**'88**), Windle (**'91**), Zander (**'91**), and Wilson (**'96**) are of especial importance. From the descriptions of the above investigators, it appears that the supernumerary digits are more frequently found on the manus than on the pes, and on both the right and left extremities than on one side only. But in those cases where the abnormalities are symmetrically placed, the structural conditions of each extremity may be different from those of the others.

The most of the cases observed fall readily into two classes:

(1) A supernumerary digit occurs on the radial side of the extremity (Fig. A); this digit may be of two or three phalanges, and in the latter case the pollex (I^b) is often composed of three elements instead of two. In most cases where an extra digit is present on the radial side of the manus, the abnormality is evidently due to a duplication of the pollex, and it is not possible to say that either of the digits is the normal thumb. These conditions hold good for the foot as well as the hand.

(2) A supernumerary digit occurs on the ulnar side of the extremity (Plate **1**, Fig. 3). This digit may be (*a*) complete, of three phalanges, and having its metacarpal articulating with the unciform (in the manus), or (*b*) incomplete, of two or three phalanges which articulate with the ulnar side or distal end of metacarpal v (minimus); in some cases the extra digit may be merely attached to the minimus loosely by a peduncle of the skin. Here again the digital variation usually occurs simultaneously on both hands, or both feet, or even on hands and feet; the conditions on the right and left sides, however, may be different. It is often impossible to tell whether the fifth or sixth digit is the true minimus. In the well known case originally described by Morand (**1773**) the muscular attachments peculiar to the minimus were transferred to

the sixth, or supernumerary, digit in the *right* hand, leading us to suppose this to be the true minimus. But in the *left* hand the sixth digit was rudimentary, and the fifth must therefore be taken as the normal minimus. These abnormalities, which occur on the ulnar side of the extremity, may therefore be best explained as due to duplication of the minimus; either one of the two digits produced may develop into an apparently normal fifth digit. To this class belong the greater number of digital abnormalities in man.

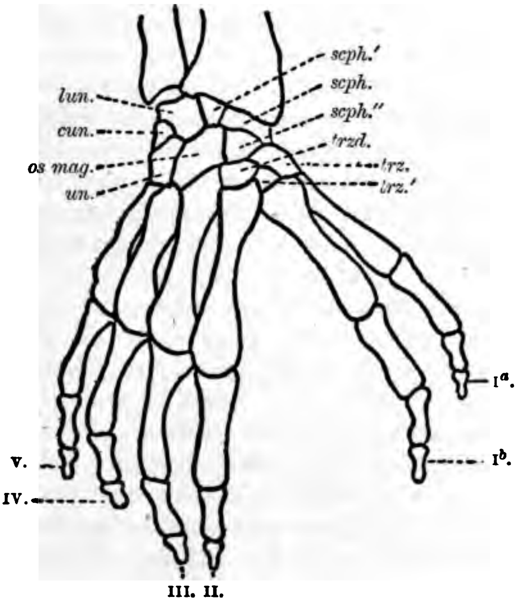

FIG. *A*.—Bones of right hand of man, showing duplicated thumb. I^a, I^b, pollices; *cun.*, cuneiform; *lun.*, lunar; *os mag.*, os magnum; *trz.*, trapezium; *trz'.*, accessory trapezium; *trzd.*, trapezoid; *scph.*, scaphoid; *scph'.*, *scph''.*, accessory scaphoids; *un.*, unciform. (After Bateson.)

There are a few cases of polydactylism in man where one extra digit has been interpolated. Bateson regards these cases as of doubtful origin.

B. OBSERVATIONS.

Through the kindness of Prof. W. F. Whitney, Curator of the Warren Museum at the Harvard Medical School, I was permitted to study the skeletal parts of twelve polydactyle extremities in man, and to obtain skiagraphs of the more important abnormalities. In every case examined the extra digit appeared on the ulnar side of the manus or pes.

The polydactyle extremities were from late foetal stages; the carpals and tarsals, therefore, show little or no calcification, and only the diaphyses of the digital elements are ossified. The specimens were on exhibition in the cases of the museum, and so could not be dissected.

Number 912 (Plate **1**, Figs. 3–6) is an interesting case. This foetus shows an extra digit on each hand and foot. In the right manus (Fig. 4) there are only five metacarpals, but the fifth shows evidence of duplication. It is abnormally large at its distal extremity, and from the ulnar side of this end projects a bony process. This process is directed somewhat proximad, and with it articulates the supernumerary digit (v^b), which is little more than half the length of v^a, and consists of but two phalanges. The other digits of this manus are apparently normal in all respects.

The structural conditions of the right foot (Fig. 6) are very similar to those of the right manus. The fifth metatarsal is short, and nearly as broad as long; a small protuberance on its ulnar side marks the point of articulation for the extra digit. The supernumerary digit shows only two ossification centres, but the incompletely calcified condition exhibited by the normal digits leads one to suppose that three phalanges might have been developed eventually. The supernumerary digit (v^b) is somewhat smaller than v^a, which may be interpreted as the normal fifth digit.

The left manus (Fig. 3) presents a different skeletal structure. The first four digits are normal as before, but the supernumerary one (v^a) is apparently located on the radial side of the normal fifth digit (v^b). The two are entirely independent of each other, and are of nearly the same size. From the appearance of the phalanges it is difficult to say which is the normal digit; however, the metacarpal of v^a is ossified at its distal end only, thus indicating that it is the interpolated digit.

The digits of the left pes (Fig. 5) resemble in their structure those of the corresponding manus. There are six distinct digits, and all of the metatarsal bones are well developed. The four external (ulnar) digits are similar in structure, each being composed of a metatarsal and two phalanges; the ossification centre of the middle phalanx has not yet appeared. The phalanges of digit v^b are smaller, and its metatarsal bone is shorter than the corresponding skeletal elements of the other digits. We may therefore consider it as the extra digit, and from the conditions found in the hands and the right foot, it seems reasonable to assume that the fifth digit has been duplicated.

These four cases of polydactylism are probably all abnormalities produced by the splitting of the fundament of the fifth digit; each instance differs slightly from the others, but the manus and pes of the right side are of somewhat similar skeletal structure, and the same is true of the left appendages. In the appendages of the right side the fifth digit is incompletely duplicated. In those of the left side the division is complete; in the manus the metacarpus of the more internal of the two digits (v^a) is amorphous, while in the pes digits v^a and v^b are both distinct and perfectly developed.

We are not warranted in assuming that either v^a or v^b is the extra digit. In the right hand v^a is better developed, in the left hand v^b, while in the feet it is difficult to distinguish any difference between the two.

Number 5809 is a foetus which, like 912, exhibits a hexadactyle condition in all four appendages. Both feet are identical in skeletal structure with the pes shown in Figure 6 (Plate **1**); the fifth metatarsal is a massive bone, as broad as long, and with it articulate two digits of nearly equal size, each consisting of two phalanges.

The right manus (Plate **2**, Fig. 8) resembles the left manus of number 912 (Plate **1**, Fig. 3); the digits v^a and v^b are distinct, but the metacarpal of v^a is amorphous. The left manus (Fig. 7) exhibits a peculiar condition. Metacarpal v is abnormally large, especially at its distal end; with it articulate the two digits v^a and v^b. v^a is apparently normal in form, size, and the number of its phalanges. v^b, however, is small, and directed proximad. Its three phalanges are small and the distal one is double.

There are, thus, three instances in which digit v is incompletely duplicated, and a single case in which there is complete splitting of this digit. Here, too, we are unable to say with certainty that either v^a or v^b is the extra digit.

In a third foetus, number 913 of the Warren Museum, only the left manus and right pes were preserved. The manus (Plate **2**, Fig. 9) has a small supernumerary digit (v^b) on the ulnar side of metacarpal v, but not articulating with it. This digit is composed of three skeletal elements, of which the two distal from their form may be interpreted as representing the first and third phalanges. The proximal element is a small nodule of bone, and may be the rudiment of a metacarpal. Metacarpal v is apparently normal, as is the digit v^a.

The right pes of the same foetus (Plate **2**, Fig. 10) has six distinct digits. Digits v^a and v^b show ossification centres of only one phalanx, while in II, III, and IV, two or three may be seen. This may indicate that the development of digits v^a and v^b had been retarded. v^b is slightly smaller than v^a, but otherwise their skeletal structure is identical.

Figures 1 and 2 (Plate 1) show a pair of feet from a fourth foetus (number 6730), in both of which six distinct digits are present. The right pes (Fig. 1) is noteworthy because of the condition of metatarsals v^a and v^b; these are nearly connected at their proximal ends, which project further proximad than any of the other metatarsals. This is another ground for assuming that v^a and v^b originated from the same fundament. In the left foot (Fig. 2) these digits are considerably smaller than the others and the proximal ends of their metatarsals also project further proximad, i. e., toward the tarsus; in both appendages the first phalanx of digits v^a and v^b is the only one showing a centre of ossification.

To sum up our observations on these twelve cases of polydactylism, we find: (1) the abnormalities in every instance affect the ulnar (fibular) side of the extremity and probably only the fifth digit; (2) in five cases metacarpal (metatarsal) V bears two digits; these may be equally well developed, or the one on the ulnar side may be more or less rudimentary; (3) in seven cases v^a and v^b are distinct from each other, although showing evidence of a common origin; either one of these digits may be completely formed, or rudimentary, and it cannot be said that one of them is the normal, and the other the abnormal, digit.

There is no evidence of reversive modifications in the polydactyle extremities an account of which has been given here. Even if we admit that the primitive ancestor of the mammalia was hexadactyle, there are still obstacles in the way of accounting for these abnormalities by reversion. A discussion of these points will be taken up in the theoretical portion of this paper.

III. Polydactylism in Carnivora.

A. LITERATURE.

Hereditary digital variations in the extremities of the cat were observed by Poulton (**'83**, **'86**); the anatomy of the skeletal parts has been studied by Bateson (**'94**); and Howe (**:02**) has given a detailed account of the general anatomy of a single case. Such abnormalities are comparatively rare in the dog, and of the few cases which have been observed I know of none which have been carefully described. Blanc

(**'93**) figures a single case in which the hallux was developed and duplicated.

In both the cat and dog the normal manus is composed of five digits, but the pollex is much reduced in size. In the pes only four functional digits are present, the hallux being represented by merely a rudiment of metacarpal I. These animals are therefore tetradactyle in the pes, and it is there only that we may look for evidence of reversion, unless we assume the existence of a hexadactyle ancestor.

Most of the digital abnormalities in Carnivora occur on the *radial* side of the manus or pes; digits II–V remain practically normal in all cases. This is an important fact when the polydactyle conditions in other animals are considered, for it shows that the digits which vary are in most cases those which have been either reduced or modified in the course of phylogenetic development.

In the pes of the cat the digital abnormalities fall into three classes:

(1) Five digits, each possessing three phalanges (Fig. *B*).

(2) Six digits, five of them possessing three phalanges each, the sixth, which resembles a normal pollex (Fig. *C*), exhibiting only two.

(3) Six digits, each having three phalanges. This is the condition of most frequent occurrence; the digits in this case are usually so formed that the pes is bilaterally symmetrical. Bateson lays considerable stress upon this symmetrical condition, which is brought about in the following manner. The distal phalanges of the normal extremities are retractile, and are always drawn back to the ulnar side of the second phalanx (that is, in the right extremity to the right, and in the left to the left). For this retraction the second phalanx of each digit is hollowed out on the ulnar side. The supernumerary digits, however, do not conform to this plan, but their ungual phalanges are drawn back to the other (radial) side of the manus or pes; consequently the second phalanx is hollowed out on the radial side to correspond. This change in the symmetry of the phalanges may extend also to the second digit (II).

In the manus of the cat we find the same three types of polydactylism and in addition a fourth type, in which there are seven digits present. Digits II–V are always normal; on the radial side of II are three extra digits, the most radial of which is amorphous (Bateson, **'94**, Fig. 86, p. 319). Torrey (**:02**) describes a similar case in which seven digits appeared, but the most radial was resorbed soon after birth. In the case described by Howe (**:02**) three complete extra digits were developed, which he considers similar in structure to digits III, IV, and V. To this class belong the majority of polydactyle cats. When six metacarpals are present in the polydactyle manus, the trapezium is almost invariably duplicated, and the length of the scapholunar is correspondingly increased; and the same is true respectively of the cuneiform and navicular in the abnormal pes.

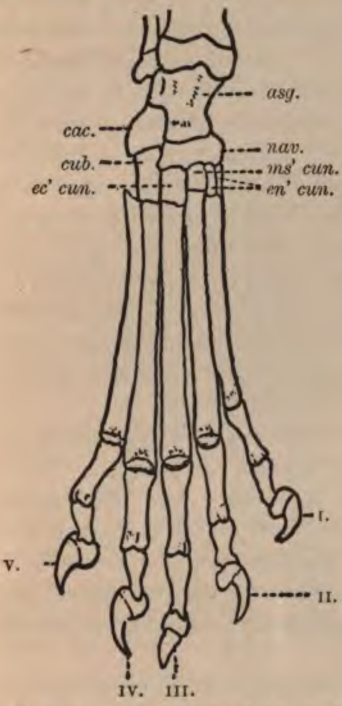

FIG. *B.* — Right pes of cat, showing hallux abnormally developed. I, hallux; *asg.*, astragalus; *cac.*, calcaneum; *cub.*, cuboid; *ec'cun.*, ecto-cuneiform; *en'cun.*, ento-cuneiform; *ms'cun.*, meso-cuneiform; *nav.*, navicular. (After Bateson.)

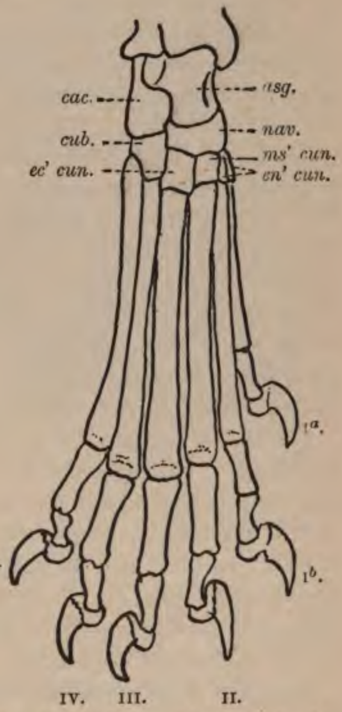

FIG. *C.* — Right pes of cat, showing duplicated hallux. I^a, I^b, duplications of hallux; *asg.*, astragalus; *cac.*, calcaneum; *cub.*, cuboid; *ec'cun.*, ecto-cuneiform; *en'cun.*, ento-cuneiform; *ms'cun.*, meso-cuneiform; *nav.*, navicular. (After Bateson.)

B. OBSERVATIONS.

Although a number of cases of polydactylism in the cat have come under my observation, it was not thought necessary to devote especial study to them, the careful work done by Bateson making that unnecessary. Polydactylism in the dog, however, has never been adequately described. On account of the difficulty of obtaining suitable material, my own work on these abnormalities is far from being complete.

Digital variations are extremely rare in the manus of the dog. The pes, however, is quite often affected, and in the larger breeds (St. Bernard, mastiff, and collie) the hallux is frequently present. All of the digital variations which have come under my observation were of the pes. As we have seen, this consists of four digits, the hallux being normally represented by only the proximal end of its metatarsal bone. The four functional digits remain unmodified in all cases of polydactylism, and the supernumerary digits occur on the radial side of digit II, as variations of the hallux. We may distinguish three classes of these abnormalities: (1) Hallux, or "dew-claw," present and formed of two phalanges articulating with the distal end of a rudimentary metatarsal. This digit does not articulate with the proximal rudiment of metatarsal I, but is merely held in place by the skin. Six cases were observed in the shepherd dog, and five cases in the St. Bernard.

(2) Hallux (Fig. *D*) presenting two well developed phalanges, of which the proximal articulates with the rudimentary metatarsal bone; this element is much longer than the normal phalanx. Three cases were observed in the mastiff, and one case in the Scotch collie.

(3) Hallux present as in (1), and more or less completely duplicated, exhibiting two phalanges and the distal rudiment of a metatarsal. This is the common condition in the pes of the St. Bernard dog. The duplication of the hallux may give rise to the rudiment of only a single ungual phalanx, or there may be complete duplication, with the formation of two similar digits (Fig. *E*. I^a, I^b). In some cases the two ungual phalanges of I^a and I^b bear but a single large claw, which, however, usually shows evidence of duplication.

The cases of polydactylism which we have observed in Carnivora may all be accounted for as modifications of the pollex and hallux. Except for the change in symmetry of the phalanges of the extremities of the cat, the rest of the manus or pes is unmodified. The conditions found in the *manus* of Carnivora are thus similar to the digital variations which occur in the hand of man. In each case a functional, but reduced, digit is affected. In man, however, it is the minimus which is normally reduced, whereas in Carnivora it is the pollex.

In the *pes* of Carnivora the conditions are somewhat different. Only a vestige of the hallux is normally present; in cases of polydactylism, this is developed and duplicated to a greater or less degree. It would seem, however, that the same underlying cause which produces polydactylism in the manus (variation of a reduced but functional digit), brings about also the digital abnormalities in the pes (variation of a vestigial digit). Whether this underlying cause is reversion, will be discussed later.

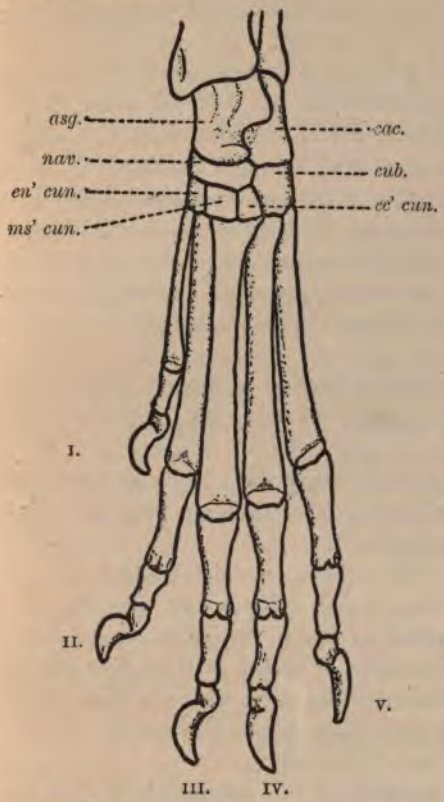

FIG. *D.*—Left pes of dog, showing hallux fully developed. I, hallux; *asg.*, astragalus; *cac.*, calcaneum; *cub.*, cuboid; *ec'cun.*, ecto-cuneiform; *en'cun.*, ento-cuneiform; *ms'cun.*, meso-cuneiform; *nav.*, navicular.

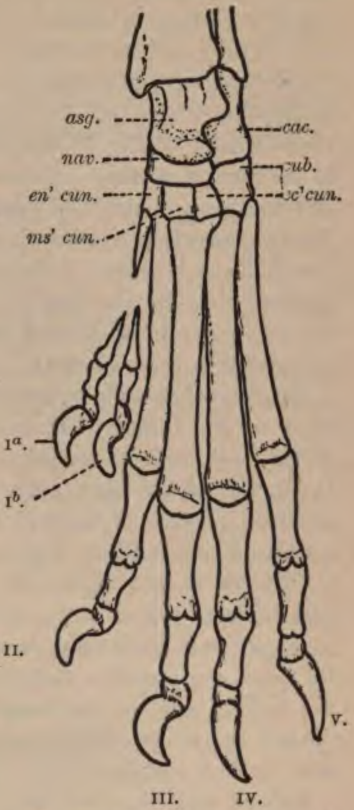

FIG. *E.*—Left pes of dog, showing duplicated hallux. I, rudimentary metatarsal of hallux; I^a, I^b, accessory digits; *asg.*, astragalus; *cac.*, calcaneum; *cub.*, cuboid; *ec'cun.*, ecto-cuneiform; *en'cun.*, ento-cuneiform; *ms'cun.*, meso-cuneiform; *nav.*, navicular.

IV. Polydactylism in the Fowl.

Although the domestic hen is tetradactyle, the fifth digit was lost so early in phylogeny that it never appears in polydactyle abnormalities. As the hallux of the pes is reduced, however, polydactylism is entirely limited to this digit; the condition is thus directly comparable to that found in the pes of the dog and cat. The skeletal parts of the polydactyle pes have been described by Cowper (**'89**), Howes (**'92**), Bateson (**'94**), and Anthony (**'99**). The last-named writer also examined the pedal musculature of the Dorking.

Polydactylism, generally rare in birds, is quite common among the Gallinaceae, especially the domestic fowl. It has become a fixed characteristic of the Dorking breed, and also occurs quite constantly in the Houdan variety. In the normal fowl, as is well known, the hallux, or first digit, is articulated at the side of the tarso-metatarsal, by a distinct rudimentary metatarsal element. Digits II–IV have their metatarsals fused together; V is entirely wanting. In nearly all cases of polydactylism in the fowl a supernumerary digit (sometimes two) occurs on the tibial side of the hallux. The abnormalities may be grouped into three classes:

(1) Pes of five digits, metatarsal I bearing a normal hallux, and tibial to this a digit of three phalanges (Cowper, **'89**, p. 249). This is the most common condition.

(2) Pes of five digits; the supernumerary digit is borne upon the proximal phalanx of the hallux instead of articulating with its metacarpal. This condition is quite frequent.

(3) Pes of five digits; the hallux being completely divided into two digits of two or three phalanges each (Howes, **'92**, Fig. 5).

Single cases have been described in which two extra digits occur. Of these, one possesses three phalanges, is placed at the tibial side of the hallux, and has an independent articulation with the tarso-metatarsus; the other exhibits only two phalanges and is formed by the more or less complete duplication of the hallux.

Bateson and Saunders (**:02**) by crossing the polydactylous Dorking fowl with white and brown Leghorn varieties, found that in the resulting offspring the polydactylous character is dominant, though not completely so, over the normal pes of the Leghorn. In addition, *the supernumerary digits of the crossbreds varied greatly from their structure in the normal Dorking.* They are described as follows (p. 97):

> "When present the two hind toes may consist, as in the normal Dorking, of a short toe, like the hallux of a 4-toed bird, with a long many-jointed digit proximal to it pointing upwards. The two, however, may often be *both* short, pointing downwards, never both long. This condition ranges through many stages of bigemination down to mere bifidity of the nail. A form very rarely seen is an *elongation* of the hallux without any extra toe being present.[1]

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[1] "[A chick has lately occurred with *a 'long' hallux bigeminus* of this sort — probably a hitherto unrecorded form.] March, 1902."

> "In such a hallux there is increase in the number of phalangeal joints. This of course corresponds to the three-jointed pollex in man. . . . In the highest form of the reduplication the short toe is itself represented by two digits, making six in all. Of this, also, there are many grades.
>
> "Lastly, any of these conditions may be seen on one foot only, while the other foot shows one of the other states or is normally four-toed. Generally speaking, however, there is a fairly close symmetrical agreement between the two feet."

Thus we see that a single cross between the Dorking and Leghorn varieties produces *all* of the polydactylous abnormalities which investigators have so far observed in the fowl.

The conditions presented are interesting and noteworthy from their structural similarity to the digital variations found in man and the Carnivora. For here, too, we find that the abnormalities are mainly confined to a reduced or modified digit, which becomes partially or completely doubled.

Howes (**'92**) and Anthony (**'99**) regard these abnormalities as due to the splitting of the hallux, not as reversions to a five or six-toed ancestor. Bateson and Saunders (**:02**, p. 137) evidently agree with them, for besides their allusions to "the reduplication" of the hallux, they class the abnormalities as "*new characters*" — "a palpable sport" (p. 137).

The significance of their experiments and the bearing of "Mendel's law" upon polydactylism will be discussed later with other theoretical considerations.

V. Polydactylism in Swine.

A. Literature.

Although polydactylism is quite common in the pig, and many cases have been recorded, few careful descriptions have been given, and those deal only with the skeletal parts. As a consequence, very conflicting statements are made by different authors concerning the causes productive of the conditions, some maintaining that polydactylism in the pig is atavistic, others that it is due to duplication of the whole foot, and still others that it is to be accounted for only by haphazard variation. Geoffroy St. Hilaire (**'32–37**), Gurlt (**'77**), Gegenbaur (**'80**), Bateson (**'94**), and Werner (**'97**) have observed instances of digital variation in swine. Otto (**'41**), Ercolani (**'81**), and Blanc (**'93**) have given good descriptions of the skeletal parts of a few cases.

Ercolani obtained data as to the skeletal structure in twenty-five cases. Of these, there was only one instance where the supernumerary digits occurred on the posterior extremity. In four cases the abnormality was found on both fore feet; and in all the specimens which he himself examined, or which were described by other observers, the extra digits occurred on the radial, or thumb, side of the manus. The abnormalities as figured by Ercolani (Tav. 1, Fig. 1–6) consist in the presence of from one to three supernumerary digits. He found also that the trapezium of the carpus was well developed in most cases, and occasionally duplicated. In two cases, however, it was entirely absent, and Ercolani therefore concludes that its presence in connection with the supernumerary digits is no proof that polydactylism is atavistic; for the trapezium is present also in most normal swine. Its absence is a deformity by defect and may occur in the normal manus.

Blanc (**'93**) considers most of the cases of polydactylism in swine as due to reversion. He figures four types: (1) Manus with an extra digit of two phalanges, representing the developed pollex (Fig. 7, p. 70). (2) An extra digit of three phalanges, which he regards as the pollex strongly developed; digit II is also abnormally large (Fig. 8). (3) Manus resembling (2), but with a small digit of two phalanges and a rudimentary metacarpal occurring on the radial side of digit I (Fig. 9). (4) Manus of six completely formed digits, the two supernumerary being large and of nearly equal size (Fig. 10). Blanc considers types (3) and (4) as reversions to the hexadactyle ancestor of mammals. Two other cases are figured to illustrate the duplication of digits I and II.

Gegenbaur (**'80**) examined two cases of polydactylism in the manus of the pig. In one specimen the carpals had been entirely removed, in the other they were partly cut away. From this fragmentary material he draws his conclusion, — that all cases of polydactylism in swine are monstrosities and not due to atavism. The conclusions of Blanc and Gegenbaur are thus completely contradictory.

If we reject the prae-pollex theory as untenable, the hexadactyle cases regarded by Blanc as reversions must be accounted for in some other way. On the other hand, Gegenbaur bases his arguments on the slender evidence of two mutilated specimens; there is need therefore of further investigation into the structural conditions peculiar to polydactyle swine, before his refutation of reversion can be accepted. In proceeding with our description of digital abnormalities in the pig we shall keep especially in mind their bearing on this question.

B. OBSERVATIONS.

The thirty-six specimens of polydactylism in the pig which are to be described were collected at The North Pork Packing establishment, Somerville, near Boston, Mass., by Mr. Charles Bullard. In certain cases the manus was severed from the arm at the inter-carpal joint, and consequently the upper row of carpals was lost. These bones, however, are fortunately not so important for study as those of the lower row, which were saved in all but one case.

In preparing the specimens for study they were first dissected merely enough to allow a spreading of the digits, and were then skiagraphed. I am indebted to the Director of the Jefferson Physical Laboratory of Harvard University, and to Professor Sabine for kindly allowing me the use of electrical apparatus for this purpose. After obtaining skiagraphs of the more important abnormal types, the muscles and nerves were dissected. Finally the bones of the carpus and metacarpus were studied and separately compared, first with the corresponding parts of the normal manus, and next with those of the fossil swine figured by Kowalevsky ('73) and by Scott ('95). By the latter means it was possible to ascertain whether or not the manus of the polydactyle pig reverts to that of more primitive fossil forms in characters other than the presence of extra digits.

Before passing to a description of the various abnormal specimens which have been studied, it may be well to examine the normal manus of the pig, and compare its skeletal elements with those of its fossil ancestors.

The pollex, or digit I, is normally absent in all living artiodactyles, and the remaining digits are arranged in two pairs (Plate 3, Fig. 11). Of these, III and IV are large, functional, and of equal length; II and V are only two thirds as long, and do not ordinarily reach the ground, II being usually the smaller. Each digit consists of a metacarpal and three phalanges. The metacarpals of digits III and IV are large and their proximal extremities interlocked; IV articulates with the ulnar side of III and is partially over-lapped proximally by the large process of the latter. In the same way a radial process from digit III overlaps metacarpal II, and, as we shall see, is a distinguishing mark in the manus of the modern pig. The phalangeal region of the manus is bilaterally symmetrical, the ungual phalanx and hoof being concave on the side facing the median plane of the manus, and convex on the side turned away from it. The hoofs of digits III and IV are united posteriorly by means of a horny pad.

The carpus (Fig. *F*) consists of two rows of four bones each; in the proximal row occur in succession, passing from the radial to the ulnar side, the scaphoid, lunar, cuneiform, and pisiform. In the distal row, which chiefly concerns us, the trapezium is most radial in position; next come in order the trapezoid, os magnum, and unciform. The trapezium (Fig. *F*, *trz.*) is rudimentary; it articulates with the postero-lateral surface of the trapezoid and ends distally in a free, pointed process, which projects distad of the proximal extremity of metacarpal II. The trapezoid (*trzd.*) is functional but small. It articulates proximally with the scaphoid, distally with metacarpals II and III. Its distal extremity is

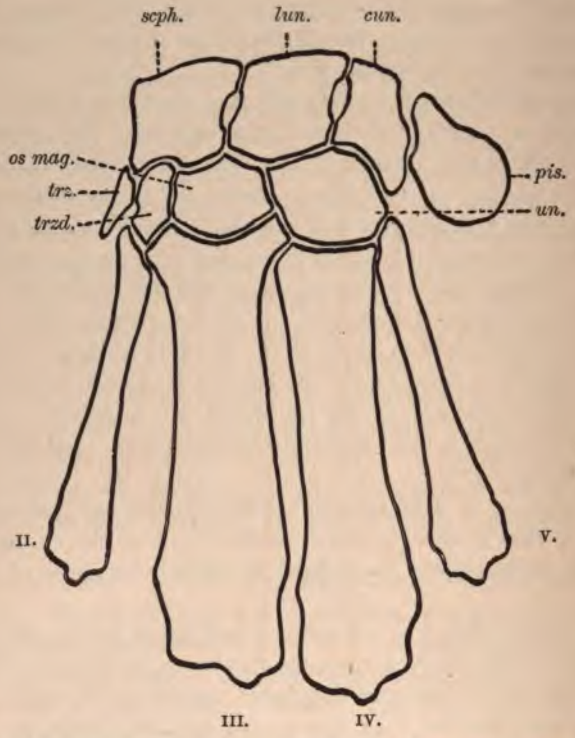

FIG. *F*. — Left normal manus of pig, showing carpals and metacarpals. II–V, metacarpals; *cun.*, cuneiform; *lun.*, lunar; *os mag.*, os magnum; *pis.*, pisiform; *scph.*, scaphoid; *trz.* trapezium; *trzd.*, trapezoid; *un.*, unciform. $\frac{8}{10}$ natural size.

wedge-shaped and divided into two facets of nearly equal size, the radial for articulation with metacarpal II, the ulnar for the large process of metacarpal III. The os magnum articulates distally with the third metacarpal only; the unciform has distally a small facet for the ulnar process of metacarpal III, a large one for metacarpal IV, and a small facet laterally placed for metacarpal V.

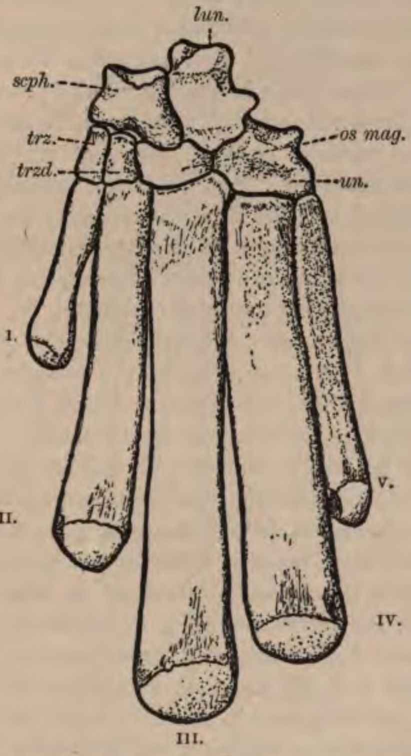

Fig. G. — Left manus of Ancodus brachyrhynchus, showing carpals and metacarpals. I–V, first to fifth metacarpals; *lun.*, lunar; *os mag.*, os magnum; *scph.*, scaphoid; *trz.*, trapezium; *trzd.*, trapezoid; *un.*, unciform. ⅔ natural size. (After Scott.)

If we compare the carpus and metacarpus of the pig with those of fossil swine (Palaeochoerus and Hyopotamus or Ancodus) figured by Kowalevsky ('73) and Scott ('95), we find some remarkable differences.

In Hyopotamus (Ancodus of Kowalevsky) the trapezium (Fig *G.*) is nearly as large as the trapezoid, and articulates superiorly with the scaphoid, inferiorly with the metacarpal of digit I. The trapezoid has only a single facet on its distal end and articulates with metacarpal II. The pollex is present and is represented in the figure by metacarpal I. Digits II and V are relatively large, especially at their proximal extremities; II is better developed than V, and occupies the whole distal surface of the trapezoid. It also articulates by a small facet with the os magnum.

The third metacarpal is longer than any of the others and proximally there is no radial process for articulation with the trapezoid. In general we may say that the digits of the fossil swine are confined chiefly to their own carpal bones, while in the pig of the present day the third metacarpal has developed a radial process which articulates with the trapezoid and has partially crowded out digit II. In the same way metacarpal IV has encroached upon the distal articular surface of the unciform, and pushed the fifth digit to one side; the third and fourth digits thus come to occupy most of the carpo-metacarpal articulation in the modern pig, a condition of evident advantage, as it strengthens the joint between the carpus and the functional digits.

If complete reversion occurs in the skeletal parts of the pig's manus, we should expect to find (1) an extra digit of two phalanges articulating with the trapezium, and (2) metacarpals II and III articulating with their proper carpal bones (trapezoid and os magnum respectively); (3) metacarpal III should be longer than IV, and without a radial process, and (4) digits II and V should be relatively larger than in the normal manus.

The normal musculature of the manus is quite complex. We need mention here only those muscles which in the polydactyle manus present variations from the normal. Anteriorly we have (1) the radial or great extensor of the metacarpus (Fig. *H*, *ext. mt'carp. mag.*). This is a large muscle and is inserted by a strong tendon into the proximal end of metacarpal III; (2) the ulnar or oblique extensor of the metacarpus (Fig. *H*, *ext. mt'carp. ob.*), a small muscle, the tendon of which crosses that of the magnum obliquely, and is inserted into the proximal end of metacarpal II; (3) the extensor communis digitorum internus (*ext. com. dg. i.*), a large muscle inserted by means of three tendons. The main tendon bifurcates, the radial portion being inserted in the third phalanx of digit II; the remaining portion of the tendon runs some distance and again bifurcates, the two branches becoming attached to the ungual phalanges of the third and fourth digits; (4) the extensor proprius internus (*ext. prp. i.*), a much smaller muscle than the preceding, is inserted by two tendons, the larger going to the radial side of the third digit, the smaller to the ungual phalanx of II; (5) extensor proprius pollicis et indicis (*ext. prp.*) is a rudimentary muscle in the pig; it arises with the extensor metacarpi obliquus, and its threadlike tendon is lost in that of the extensor communis digitorum internus.

Of the posterior muscles we may mention (1) the flexor perforatus, or superficial flexor of the digits (Fig. *I*, *flx. perf.*); this is composed of two distinct parts, the tendons of which are inserted into the second phalanges of digits III and IV. These tendons form two sheaths for the large tendons of the flexor perforans muscle (*flx. perf.!*), the deep flexor of the

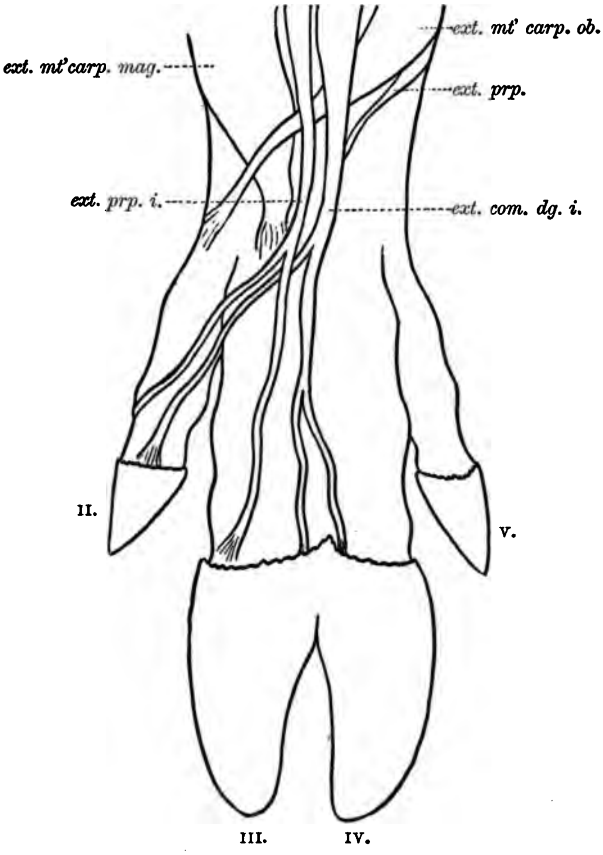

FIG. *H.* — Left normal manus of pig, showing extensor muscles. *ext. com. dg. i.*, extensor communis digitorum internus; *ext. mt'carp. mag.*, extensor metacarpi magnus; *ext. mt'carp. ob.*, extensor metacarpi obliquus; *ext. prp.*, extensor proprius pollicis et indicis; *ext. prp. i.*, extensor proprius internus. ⅔ natural size.

digits. This divides into four tendons, two large and two small; the two large ones, after passing through the sheaths formed by the perforatus, are inserted into the ungual phalanges of digits three and four; the two smaller tendons are attached similarly to the second and fifth digits.

As regards the innervation of the normal manus, we need concern ourselves with the condition of the median nerve only, by which the digits

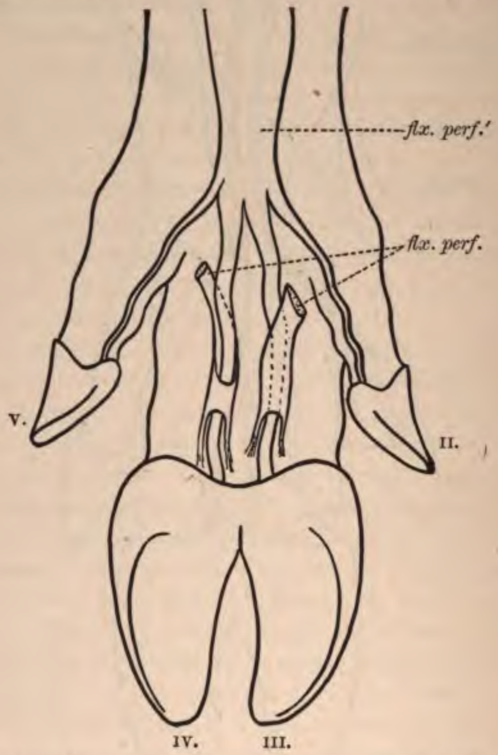

FIG. *I.* — Left normal manus of pig, showing flexor muscles. *flx. perf.*, tendons of flexor perforatus; *flx. perf'.*, flexor perforans. ⅔ natural size.

are chiefly supplied. The trunk of the median nerve (Fig. *J*, *n.m.*) passes between the two flexor muscles at the carpal joint; nearly at a level with the proximal ends of metacarpals II and V it gives off two lateral branches (2, 5) to supply these digits. The main nerve, continuing distally, soon separates into two large branches (3, 4), which pass together along the region between digits III and IV, to which they are distributed. The lateral branches (2, 5) before passing to their respective digits divide, the larger of the resulting branches innervating the lateral portions of the third and fourth digits.

In pentadactyle animals (Carnivora and Primates) the median nerve gives off a fifth branch radial to 2 of the pig's manus, which divides and supplies the thumb and index. No remains of such a nerve branch could be detected in dissections of the normal manus of the pig.

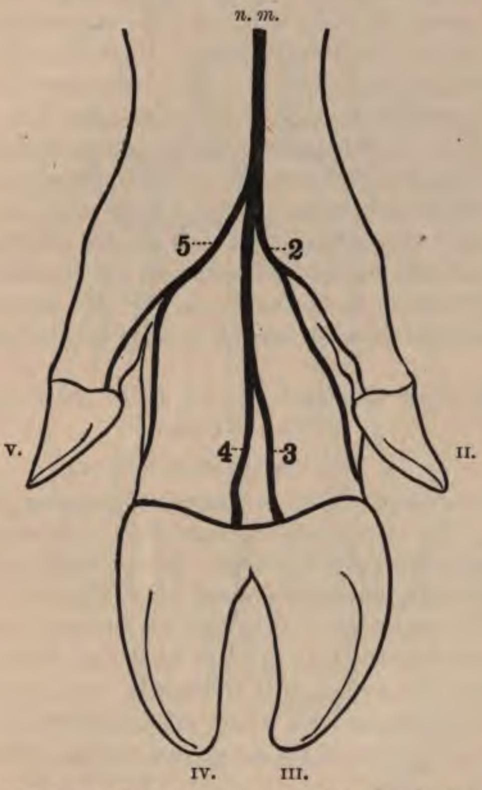

FIG. *J.* — Posterior view of the left normal manus of pig, showing innervation. *n. m.*, median nerve; 2–5, four branches of the median nerve supplying the corresponding digits. ⅔ natural size.

If the polydactyle manus of swine is due to reversion, we might expect to find reversive modifications in the muscles and nerves, as well as in the skeletal parts.

The extensor of the thumb and index might be fully developed and its tendon inserted into the phalanges of digits I and II, as in pentadactyle animals; the oblique extensor of the metacarpus might be found inserted into metacarpal I, and the flexor perforans muscle might send a tendon to digit I. The pollex, if thus supplied with muscles, should be innervated by a branch from the radial side of the median nerve. In examining the following cases of polydactylism in the manus of the pig, we shall see whether these theoretical conditions are ever fulfilled.

Of the thirty-six instances of polydactylism which were studied, all were of the manus; in every case, also, the supernumerary digit occurred on the radial side of the extremity. Digit II is abnormal in some cases. The abnormalities might be divided into numerous types according to the number and condition of the extra digits; but as these types grade into one another, we shall attempt to distinguish but two classes: (1) cases in which the supernumerary parts are distinct from, and independent of, the normal digits; (2) cases where they are more or less closely connected with digit II. We shall see that even these are artificial groups, and that intermediate conditions link together the two. In the following descriptions, we shall begin with the simplest forms, and pass in succession to the more complex types of polydactylism.

1. *Manus in which the Supernumerary Digits are Independent of the Normal Digits.*

a. One Supernumerary Digit.

The simplest example of this condition is represented by a single case (Plate 4, Fig. 12). Externally the extra digit (I) is inconspicuous, but originally bore a small claw-like hoof. It is composed of two rudimentary phalanges and a spheroidal element, which apparently represents the distal end of a metacarpal. This does not articulate with the second metacarpal, but is merely held in place by fibrous tissue and the skin.

In the carpus the trapezium is abnormally long; it articulates with the trapezoid laterally, and has a facet proximally for the scaphoid; in other respects the bones of the manus are normal. The muscles and nerves are unmodified.

Figure 13 (Plate 5) shows a manus in which the pollex is fully developed. Of this type, four cases were examined. The pollex (I) is smaller than digit II and consists of the metacarpal and two phalanges. The metacarpal bone articulates with the trapezium, which is abnormally large and has three facets: a distal for metacarpal I, a lateral for the trapezoid, and a proximal for the scaphoid. The relations of the bones of this digit to those of the rest of the manus are thus identical with the conditions found in fossil swine and in other pentadactyle animals.

On examining the other skeletal elements of the manus, in order to determine whether they show reversive modifications, one is at once struck by the form of the trapezoid (Fig. *K*, *trzd.*). Although of normal size, there is a remarkable change at its distal end; instead of projecting as a wedge between metacarpals II and III (see normal manus, Fig. *F*, *trzd.*, p. 264), and presenting two distal facets nearly equal in size, there is only one articular surface, which is slightly convex and occupied entirely by metacarpal II. The trapezoid barely touches metacarpal III; its form and relations to the other skeletal parts thus approach those of the trapezoid of fossil swine (Fig. *G*, p. 265).

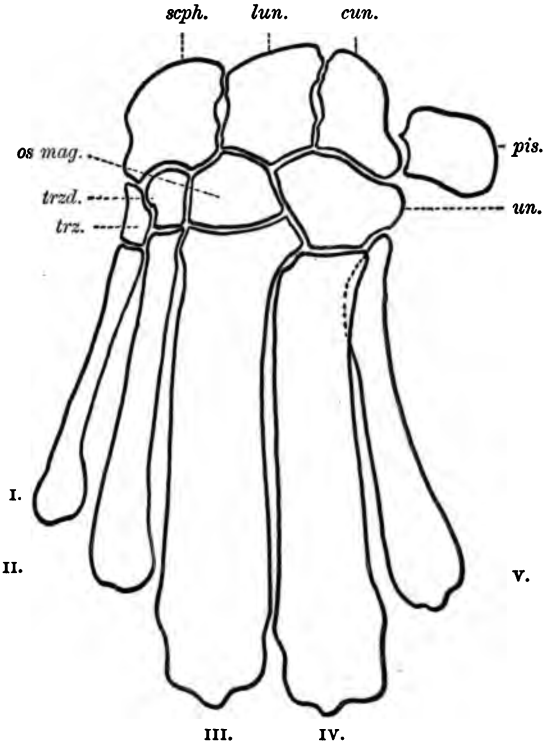

FIG. *K*. — Anterior view of left polydactyle manus of the pig, showing carpals and metacarpals. I–V, first to fifth metacarpals; *cun.*, cuneiform; *lun.*, lunar; *os mag.*, os magnum; *pis.*, pisiform; *scph.*, scaphoid; *trz.*, trapezium; *trzd.*, trapezoid; *un.*, unciform. ¾ natural size.

In correspondence with these carpal variations, the metacarpals show some changes. The metacarpal of digit II is slightly larger than normal, and its proximal end is relatively large. In digit III the radial process of the metacarpal bone, a special character of the manus in recent swine, is greatly reduced, and as a result scarcely touches the trapezoid, while metacarpal II comes in contact posteriorly with the os magnum. The trochlear ridges of the metacarpals are retained, and the phalanges show no modifications in form.

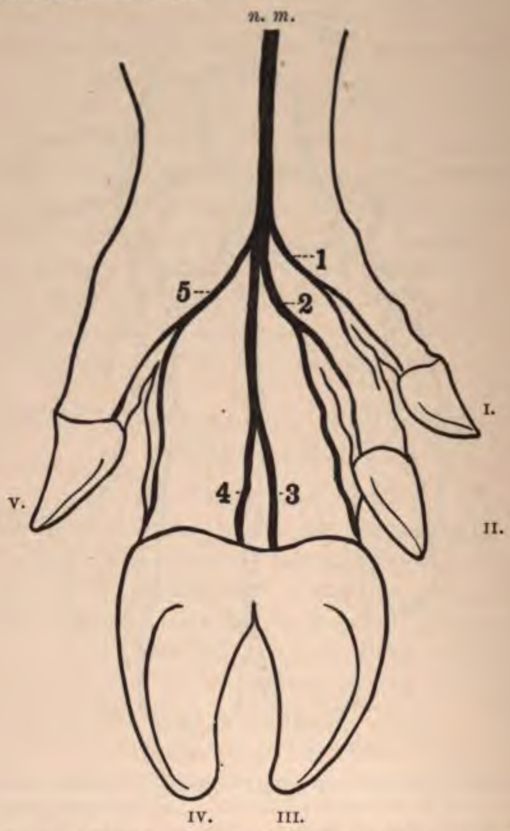

FIG. *L.* — Posterior view of left polydactyle manus of the pig, showing innervation. *n. m.*, median nerve; 1, branch of median nerve supplying the supernumerary digit (I). ⅔ natural size.

The muscles are not much modified, for the extra digit is small and functionless. In two instances, however, the tendon of the extensor metacarpi obliquus muscle is inserted into the proximal end of digit I. This is an interesting condition, as in normal five-toed animals this muscle is likewise always inserted into the metacarpal of the pollex.

The innervation of the extra digit is also noteworthy. The median nerve (Fig. *L*, *n.m.*) gives off on the radial side of its normal divisions a small additional branch (1). This divides like the other branches, sending one division to digit II and the other to the pollex.

Closely resembling the cases just described, are two instances of polydactylism in which the trapezium is fused to the supernumerary metacarpal. The extra digit is very small, and the metacarpal articulates well up on the radial side of the trapezoid. This condition favors the theory that the trapezium of the manus of the pig may represent the carpal element plus the rudiment of digit I.

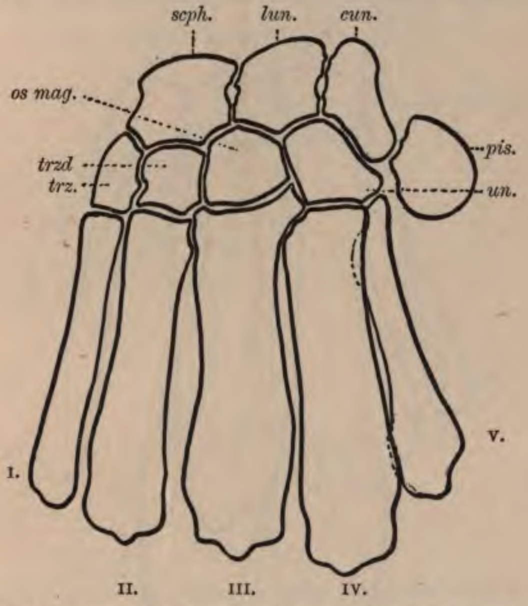

FIG. *M*. — Anterior view of left polydactyle manus of the pig, showing carpals and metacarpals. I–V, first to fifth metacarpals; *cun.*, cuneiform; *lun.*, lunar; *os mag.*, os magnum; *pis.*, pisiform; *scph.*, scaphoid; *trz.*, trapezium; *trzd.*, trapezoid; *un.*, unciform. $\frac{3}{4}$ natural size.

Taking now a step further in our series, we come to a condition in which the extra digit is still larger and consists of three phalanges (Plate 6, Fig. 14). The four cases of this type studied showed practically the same anatomical conditions. Digit II is relatively larger. Digit I articulates with the trapezium, which is large and has facets for the trapezoid, scaphoid, and metacarpal I (Fig. *M*, *trz.*). The trapezoid has become enlarged to correspond with the increased size of its digit (II); it articulates chiefly with metacarpal II, its facet for III being small. The radial process of metacarpal III is considerably reduced. In another case (Plate 7, Fig. 15) the trapezium was fused to the proximal end of metacarpal I.

In Figure 16 (Plate 8) is shown a manus which exhibits an extremely interesting structure. The extra digit is identical in its structure with that of the manus figured in Plate 6, but the second digit is very strongly developed, and is in fact more massive than either III or IV.

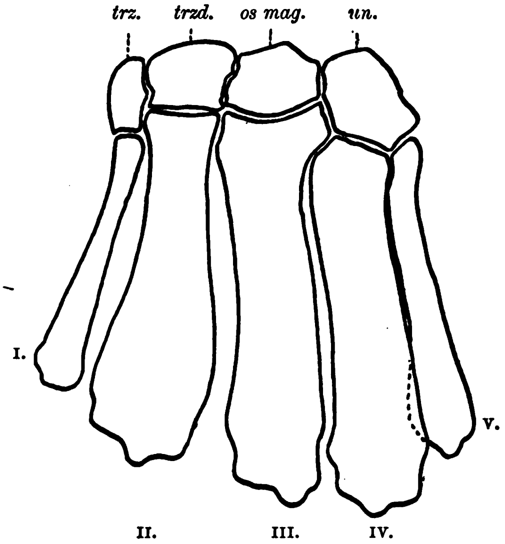

FIG. *N.*—Anterior view of left polydactyle manus of the pig, showing lower row of carpals and metacarpals. I–V, metacarpals; *os mag.*, os magnum; *trz.*, trapezium; *trzd.*, trapezoid; *un.*, unciform. ¾ natural size.

Its hoof is large, convex on its radial, and flat on its ulnar surface; it is entirely independent of the hoof of digit III. The third phalanx of digit II is also convex on its radial side; that of digit III is indifferent, and its hoof is flat on either side. The other digits are apparently normal. Of the carpals, the trapezium (Fig. *N*, *trz.*) is large and articulates with the scaphoid, trapezoid, and metacarpal I. The trapezoid (*trzd.*) is nearly as large as the os magnum (*os mag.*), and its single distal facet articulates with only metacarpal II.

Of the metacarpals, I is small but well formed; II is larger than III at its distal end and shows evidence there of pathological hypertrophy.

Metacarpal III has scarcely any radial enlargement at its proximal end and does not articulate with the trapezoid.

Turning now to the musculature of these cases in which the supernumerary digit is composed of three phalanges, we find that in every case the extensor metacarpi obliquus (Fig. *O*, *ext. mt'carp. ob.*) has shifted its insertion from the second to the first metacarpal; the extensor proprius pollicis et indicis (Fig. *O*, *ext. prp.*), which normally is extremely rudimentary, is in two cases inserted into the distal phalanges of digit I.

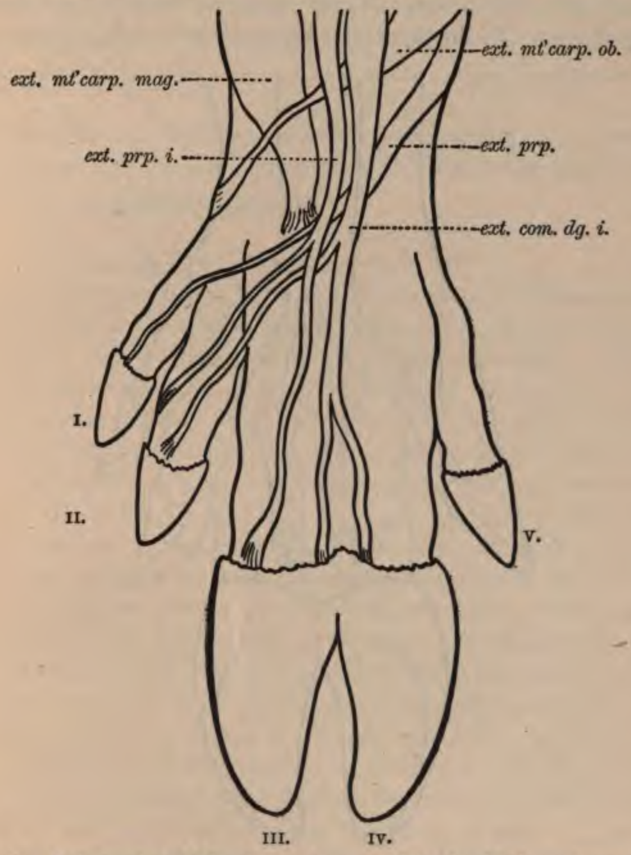

FIG. *O.* — Anterior view of left polydactyle manus of the pig, showing extensor muscles. *ext. com. dg. i.*, extensor communis digitorum internus; *ext. mt'carp. mag.*, extensor metacarpi magnus; *ext. mt'carp. ob.*, extensor metacarpi obliquus; *ext. prp.*, extensor proprius pollicis et indicis; *ext. prp. i.*, extensor proprius internus. ⅔ natural size.

The flexors exhibit a very interesting condition; in all cases the deep flexor, or perforans (Fig. *P*, *flx. perf.'*), sends a small tendon to the extra digit; this apparently is not formed by the division of the tendon which supplies digit II, but is given off from the main tendon independently and more proximally. It may represent the radial portion of the flexor perforans. In the three cases where the second digit is abnormally large, the tendon of the perforans supplying this digit is much stronger than usual. The superficial flexor, or perforatus, is normal in most cases, but in one instance has three insertions, an extra tendon going to the second digit.

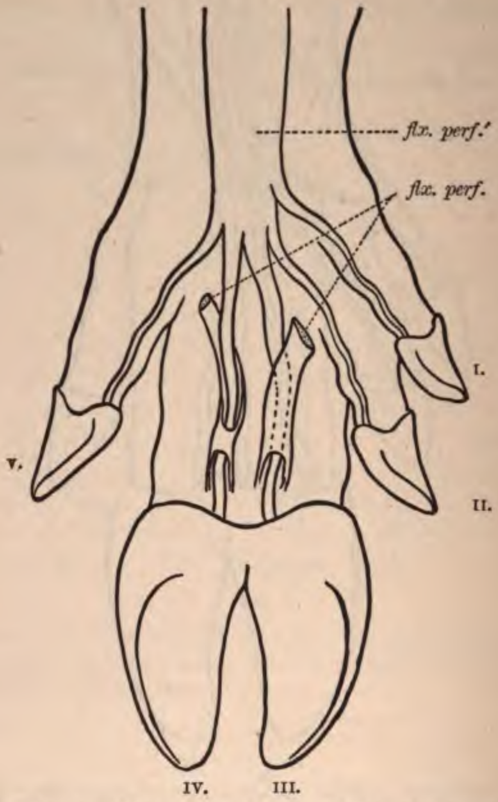

FIG. *P*. — Posterior view of left polydactyle manus, showing flexor muscles. *flx. perf.*, flexor perforatus; *flx. perf'.*, flexor perforans. ⅔ natural size.

The innervation of these cases is identical with that shown in Fig. *L*.

A still greater development of digit I was exhibited in two of the cases studied. Such a manus is shown in Figure 17 (Plate **9**). The three phalanges and metacarpal of digit I are larger than those of digit II; the digit is borne on the trapezium, which is also large and articulates with the scaphoid and trapezoid. The other skeletal elements of the manus are normal in structure. The musculature and innervation of these two cases were identical with those shown in Figures *O*, *P*, and *L*.

The cases thus far described possess but one extra digit. Continuing the examination of the polydactyle series, it is found that this digit may be partially or completely doubled.

b. TWO SUPERNUMERARY DIGITS.

Ten cases were studied. From the intermediate conditions found, it seems probable that these forms of polydactylism are further modifications of those instances which have but a single extra digit. Figure 18 (Plate **10**) shows the skeletal structure of one of the simplest of these conditions. The anatomy of the manus resembles in general that seen in Figure 17 (Plate **9**). Metacarpal I is large and articulates with the trapezium, but instead of a single set of phalanges two series of bones are present. One of these series (Plate **11**, Fig. 19, I^b) may be small, pollex-like and composed of two phalanges, or both sets may be of nearly equal size and each consist of three elements (Plate **10**, Fig. 18, I^a, I^b). Of four cases examined, three showed the latter condition. The trapezium and scaphoid are abnormally large in all cases. The musculature is like that of the pentadactyle manus (Figs. *O*, *P*), but the tendons which there supply the single extra digit may here bifurcate, and be inserted into the two digits. The nerve branch which supplies the first digit in Figure *L* also divides (Fig. *Q*), so that in these cases there is undoubtedly a duplication of digit I. Eliminating this digit, the rest of the manus, save for the large size of the trapezium, would be entirely normal.

We now pass to a polydactyle condition in which digit I is completely divided. The manus shown in Figure 20 (Plate **12**) is interesting as being a stage intermediate between the preceding cases and a complete hexadactyle condition, and as additional evidence that the two extra digits are produced by the duplication of digit I. For in this case, although each is composed of a metacarpal and three phalanges, I^a and I^b are alike in size and form; still more noteworthy is the fact that the two ungual phalanges are enveloped in a single hoof, and that the two metacarpals articulate with the single trapezium. This carpal is large;

the trapezoid, on the contrary, is small and laterally compressed, as is also the proximal end of metacarpal II.

The tendons of the muscles and the nerve of digit I bifurcate (Fig. *Q*, 1).

This intermediate stage leads up to conditions in which there are two complete and entirely distinct digits. The duplication may extend even to the carpus, and the two digits thus formed may be nearly as large as the functional digits (III and IV) of the manus. Six such cases were examined. In the typical condition (Plate **13**, Fig. 21) the supernumerary digits (I^a, I^b) are somewhat smaller than III and IV. Each

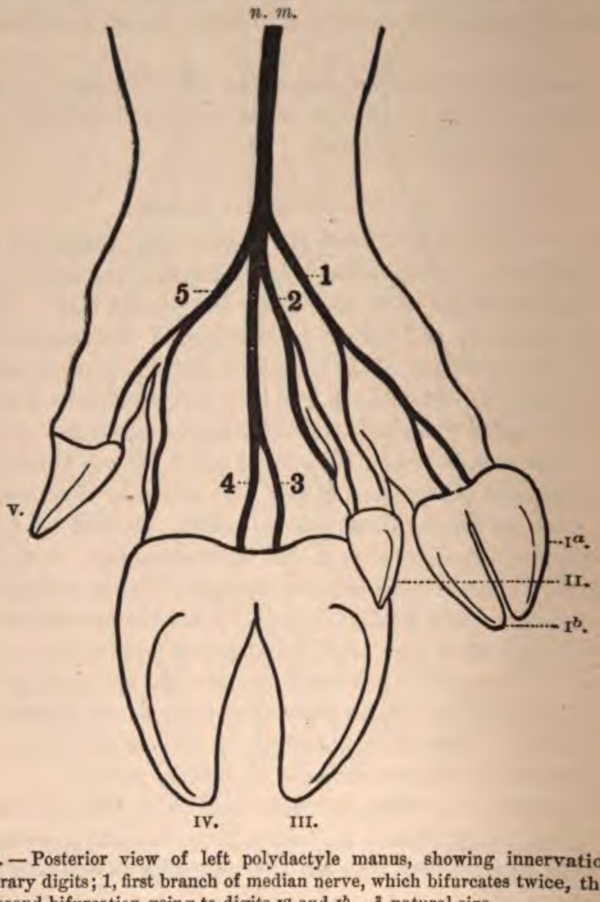

FIG. *Q*. — Posterior view of left polydactyle manus, showing innervation. I^a, I^b, supernumerary digits; 1, first branch of median nerve, which bifurcates twice, the branches from the second bifurcation going to digits I^a and I^b. ⅔ natural size.

bears a large hoof, and the two hoofs are connected posteriorly by a cushion of horny tissue, as are the functional digits. The trapezium, which articulates with both extra digits, is very large, and shows evidence of duplication; the scaphoid also is abnormally large and broad. The trapezoid is narrow, being flattened by the large trapezium; the proximal end of metacarpal II also suffers in this respect.

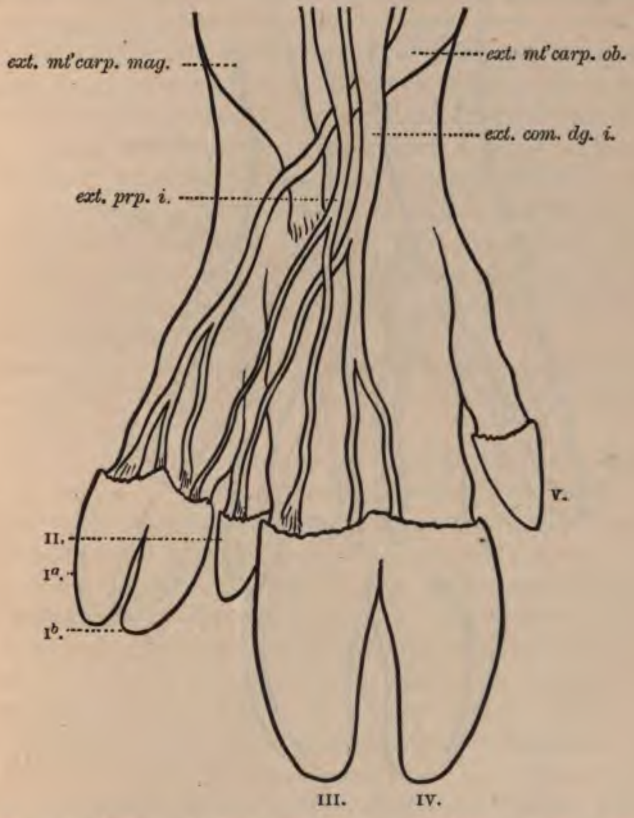

Fig. *R.* — Anterior view of left polydactyle manus of the pig, showing extensor muscles. *ext. com. dg. i.*, extensor communis digitorum internus; *ext. mt'carp. mag.*, extensor metacarpi magnus; *ext. mt'carp. ob.*, extensor metacarpi obliquus; *ext. prp. i.*, extensor proprius internus; I^a, I^b, supernumerary digits. ⅓ natural size.

When I^a and I^b are so large as to be functional, the muscles of the manus show some important modifications. Extensor proprius internus (Fig. *R*, *ext. prp. i.*) sends a tendon to I^b; extensor metacarpi obliquus (*ext. mt'carp. ob.*) is large, and its tendon, instead of being inserted as normally into the proximal end of metacarpal II, continues down to the distal phalanges of the supernumerary digits, into which it is inserted by three slips. In two cases this muscle was strengthened by a strong slip from the great extensor of the metacarpus. This is an interesting case of adaptation, and shows what a strong influence the functional capacity of the digits has on the development and structure of their muscles.

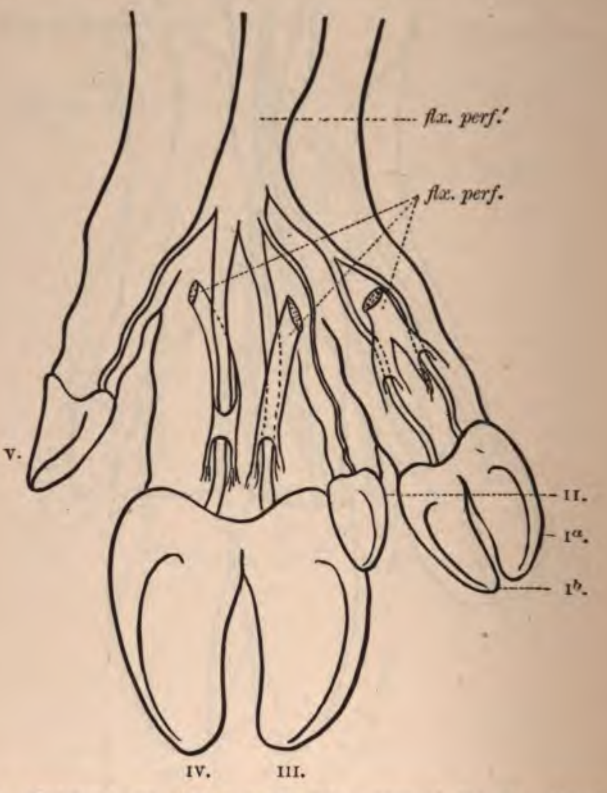

FIG. *S.*—Posterior view of left polydactyle manus of the pig, showing flexor muscles. *flx. perf.*, flexor perforatus tendons; *flx. perf'.*, flexor perforans; I^a, I^b, supernumerary digits. ¾ natural size.

Of the flexor muscles, the perforans (Fig. *S*, *flx. perf.'*) gives off a large tendon to the extra digits; this divides, and a branch is inserted into each ungual phalanx. The flexor perforatus (*flx. perf.*) also sends a large tendon to the extra digits, which bifurcates in the region of the second phalanges and forms a sheath for each division of the perforans tendon. The innervation is shown in Figure *Q*.

With the increase in size of the extra digits of the polydactyle series, goes a corresponding decrease in the size of digit II. It is apparently reduced, and partially, sometimes completely, atrophied on account of the abnormal development of the supernumerary parts. In a case figured by Bateson (**'94**) the middle portion of metacarpal II is gone. In two front feet, from a single animal, I found that the left manus was like that shown in Figure 20, the trapezoid and proximal end of metacarpal II being reduced; in the right manus, however, metacarpal II was completely atrophied, but the three phalanges persisted and were of nearly normal size. The trapezoid remained as a small flattened bone, articulating chiefly with metacarpal III. The reduction is carried a stép further in another case, in which the three phalanges of digit II are present, but exceedingly small, and the hoof reduced to a claw-like vestige (Plate **14**, Fig. 22, II).

The nerve branch which normally supplies the second digit innervates this vestige (Fig. *T*, 2), making it reasonably certain that we have to do with the rudiment of digit II.

Figure 23 (Plate **15**) represents the skeletal parts of a manus in which the second digit has apparently atrophied completely. Three specimens were examined which exhibited this condition. Such cases have been described as duplications of digit II, but a careful study of the manus shows that this is not the case. If we compare Figure 23 with Figure 22, the resemblance between the skeletal parts of the extra digits is striking. In each case they both articulate with the trapezium, and digit I^b has taken nearly complete possession of the distal facet of the trapezoid, which is normally occupied by digit II. The trapezoid itself is narrow and smaller than the trapezium; the scaphoid in Figure 23 is divided into two elements, a condition which is found *only when two large functional digits are added to the normal number*. Other important facts are that digits I^a and I^b are of nearly equal size, symmetrical with reference to each other, and bear hoofs which are connected posteriorly by a pad of horn.

The musculature and nerves also afford good evidence in favor of this interpretation. The tendons which are normally inserted into the second digit are wanting here. The second branch of the median nerve (Fig. *U*, 2), which normally supplies digit II, still sends a large branch to the radial side of digit III and may thus be identified. But dissections failed to disclose the small nerve which usually supplies the second digit. We can only conclude, then, that digit II, together with its accessories, has atrophied. This manus is therefore only pseudo-pentadactylous, and belongs in reality to the hexadactyle abnormalities. This conclusion is made possible only through the completeness of the polydactyle series which I have studied, and emphasizes the futility of attempting to obtain general results from single cases of polydactylism. Except for the intermediate stages at my disposal, the true significance of the structural conditions shown in Figure 23 could only have been guessed at.

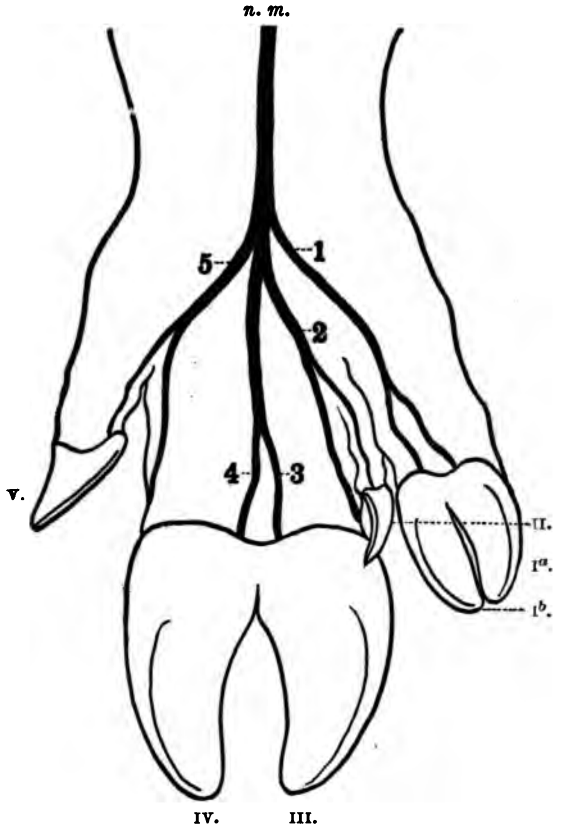

FIG. *T.* — Posterior view of left polydactyle manus of the pig, showing innervation. I^a, I^b, supernumerary digits; 1, first branch of the median nerve, which bifurcates to the extra digits; 2, second branch, a division of which innervates the rudimentary digit II. ⅔ natural size.

Conditions are rare where more than two supernumerary digits occur in the polydactyle manus. Such a condition, however, is shown in Figure 24 (Plate **16**). Digits I^a and I^b are well formed and each consists of three phalanges, but between them, and articulating with the proximal end of the second phalanx of I^b, is an elongated bone, which, from its position and form, may represent a first phalanx fused to a portion of a metacarpal. In the carpus we find the trapezium represented by two elements (*trz.*, *trz.'*), and the scaphoid is also duplicated.

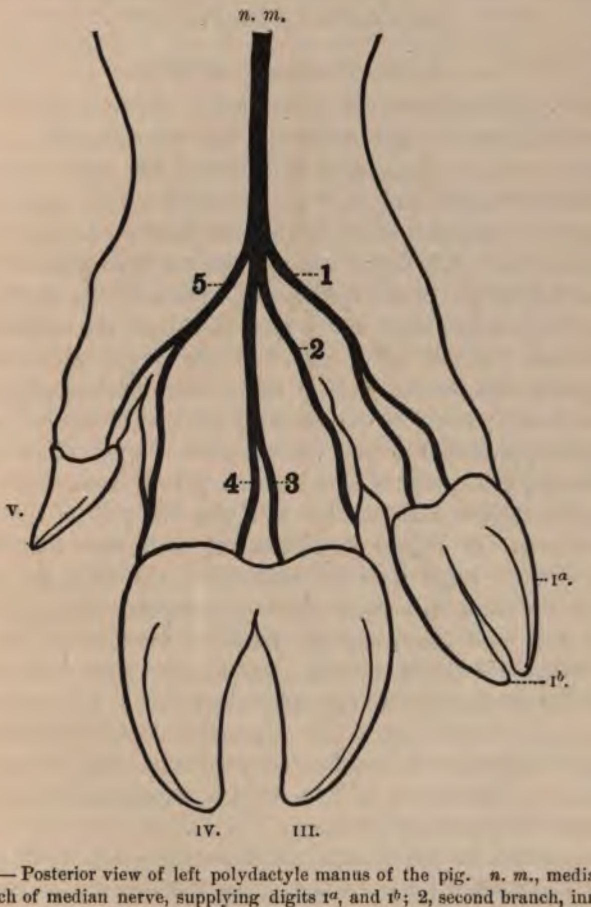

FIG. *U.* — Posterior view of left polydactyle manus of the pig. *n. m.*, median nerve; 1, first branch of median nerve, supplying digits I^a, and I^b; 2, second branch, innervating digit III; its small radial division is wanting. ⅔ natural size.

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The other skeletal elements of this manus are normal. The musculature and innervation are identical with the conditions shown in Figures *Q*, *R*, and *S*.

2. *Manus in which the Supernumerary Parts may be more or less closely connected with Metacarpal II.*

a. One Supernumerary Digit.

This condition was observed in five cases. From a typical example (Plate **17**, Fig. 25) it might be inferred that all these cases were to be interpreted as mere duplications of digit II. The extra digit (I) possesses three phalanges and is of the same size as II. Both are borne on the same metacarpal, which is large and has two articular condyles at its distal end. The digits, however, are not symmetrical with each other, as we should expect if they had resulted from duplication of digit II; in both, the hoofs and ungual phalanges are concave on the ulnar, convex on the radial side. In the carpus *the trapezium is larger than normal*, and articulates above with the scaphoid, and below with the radial portion of the proximal facet of metacarpal II. This condition is represented by only a single case. In four other specimens the skeletal parts exhibited very interesting conditions which serve to connect this class of abnormalities with the first part of the series we are describing. In Figure 26 (Plate **18**) it is seen that the extra digit (I) is much larger than the second (II), but, as in the preceding case, both are borne on a single large metacarpal. They are not symmetrical with each other, and on examining carefully the metacarpal, a dark irregular line will be seen, running nearly the whole length of the bone and dividing it into two unequal portions. This line of separation, so clearly brought out in the skiagraph, is not, of course, a surface marking but represents a complete bony septum. The two components into which the metacarpal is thus divided, correspond in size with the digits which they respectively bear.

The structure of the carpals furnishes important evidence as to whether the extra digit is formed by the splitting of II. If this were the case, the trapezoid should show signs of duplication, while the trapezium should remain normal. On the contrary the trapezium is large and *fused to the* trapezoid. Comparing Figure 26 with Figure 17 (Plate **9**), the similarity of the skeletal structures is striking, and we can but conclude that the manus shown in Figure 26 differs from that shown in Figure 17 only in the fusion of its trapezium and trapezoid, and of its first and second metacarpals. This view is borne out by another manus, in which the trapezium is fused to the proximal end of the compound metacarpal, and also by a case figured by Ercolani ('**81**, Tav. I, Fig. 2). In this instance digit II is of normal size, and its metacarpal is fused with metacarpal I along its proximal half only. This element (I) is large and bears three large phalanges. The compound bone formed by the fusion of metacarpals I and II *articulates above with the trapezoid, which is normal, and also with the trapezium, which is abnormally large.* If metacarpals I and II of the manus shown in Figure 17 were fused at their proximal ends, we should have a condition identical with that figured by Ercolani.

The evidence of the skeletal parts is in the main confirmed by the arrangement of the muscles and nerves. The condition of the muscles is similar to that of cases where the extra digit is distinct (Figs. *O*, *P*, pp. 275, 276). In the five cases dissected, digit II retained its own peculiar muscles. In one case all the muscles were normal; and in one instance the most radial tendon of the flexor perforans (Fig. *P*, *flx. perf.'*), which is normally inserted into digit II, bifurcates and is attached to digit I as well. In all cases the supernumerary digit was innervated by a *special branch* given off independently from the radial side of the trunk of the median nerve, as in pentadactyle animals (Fig. *L*, 1, p. 272). There is little ground, therefore, for regarding these cases of polydactylism as due to duplication of digit II; on the contrary, there is direct evidence against this view. (1) Digit I varies in size, while digit II always remains normal; (2) they are not symmetrical with each other; (3) the divisions of the metacarpal bone are unequal; (4) the trapezoid is not duplicated nor increased in size; (5) there is no general duplication of muscle tendons; (6) the extra digit is innervated by an independent branch of the median nerve.

In favor of the assumption that the extra digit represents the pollex independently developed and later fused to metacarpal II, is the fact that the trapezium is of abnormal size, and always articulates with the radial portion of the proximal facet of the compound metacarpal; also the striking resemblance of the skeletal, muscular, and nervous structures to those of the cases in which the extra digit does arise independently.

b. Two Supernumerary Digits.

Three cases were observed representing two types. Of the simplest condition there was but one case. In this manus digit I^a (Plate **19**, Fig. 27) consists of two small phalanges and the distal end of a metacarpal bone; digits I^b and II are of nearly equal size, each composed of three phalanges and borne on a single large metacarpal. I^a and I^b are enclosed in the same hoof, which shows evidence of duplication.

The phalanges of digit II are of normal size and form; the carpals are practically normal, but the trapezium articulates with the proximal end of the compound metacarpal, and ends in a free distal process. The musculature of digit II is normal. The extensor proprius pollicis et indicis divides and is inserted into the distal phalanges of both I^a and I^b. The flexor perforans gives off an independent tendon to digit I^b. The innervation of the manus (Fig. *V*) is identical with that of cases in which the two extra digits are entirely distinct from II (Fig. *Q*).

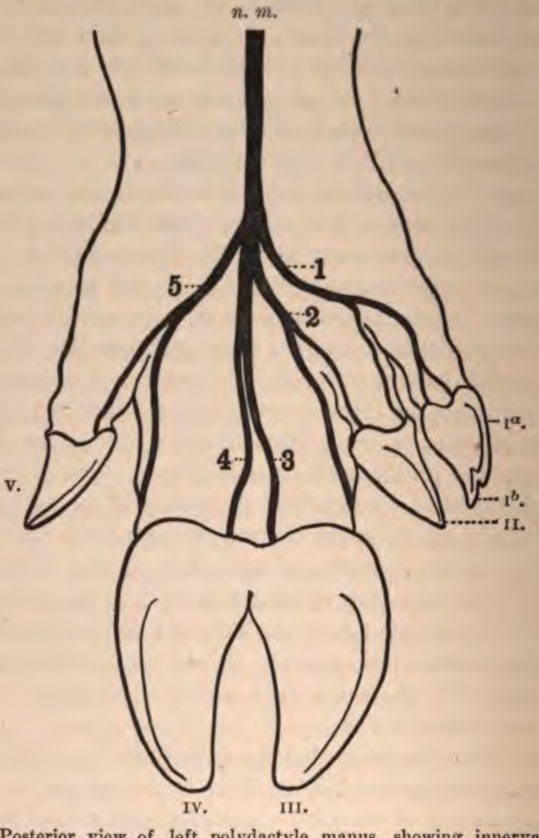

FIG. *V*. — Posterior view of left polydactyle manus, showing innervation. I^a, I^b, supernumerary digits; *n. m.*, median nerve; 1, first branch of median nerve supplying digits I^a and I^b. $\frac{2}{3}$ natural size.

This abnormality may be accounted for in two ways: Either (1) digit I^a represents the developed pollex, and I^b is formed by the duplication of digit II, or (2) digits I^a and I^b are duplications of the pollex, and the metacarpal of I^b is secondarily fused to that of digit II. The first hypothesis is supported by the similarity in structure of digits I^b and II, their symmetry with reference to each other, and the differences existing between I^a and I^b. The second view, however, is supported (1) by the fact that the extra digits are enclosed in the same hoof, and therefore probably developed together, (2) by the fact that the trapezium articulates with the compound metacarpal, and (3) by the structure of the muscles and nerves.

To another type belong two cases in which digit I^a is completely developed and articulates with the carpus (Plate **20**, Fig. 28). Digits I^b and II are borne on a single large metacarpal, but I^b is much the larger. The phalanges of II are of normal size and unsymmetrical with those of I^b. The ungual phalanges of both I^a and I^b are enclosed in separate hoofs, and are symmetrical with each other, although differing somewhat in size. The trapezium is large, and articulates with metacarpal I^a and with a portion of the compound metacarpal. The musculature and innervation of this manus are similar to those of the foregoing case.

Our view that these abnormalities are due to duplication of the pollex and the subsequent fusion of the metacarpal of I^b to that of II, is favored by the structure of a manus figured by Otto (**'41**, Tab. 26, Fig. 12). In this case there are two extra digits of three phalanges; I^a is borne on a distinct metacarpal, which articulates with the trapezium, and I^b on a metacarpal which is almost completely fused to metacarpal II. Digit II is of normal size. The phalanges of I^a and I^b *form a single* series of three bones, each of which is incompletely divided into two; the ungual phalanx evidently bore a single hoof. The trapezium articulates with metacarpal I^a and with two-thirds of the proximal surface of the compound metacarpal. The trapezoid is smaller and articulates with the remaining third of the proximal facet of the large metacarpal bone. In this manus, therefore, the digits I^a and I^b evidently developed together, and the fusion of metacarpal I^b to that of II was of subsequent occurrence. This being the fact, it is very probable that the foregoing cases which we have examined were produced in a similar manner.

Having now briefly described the types of digital variation in the manus of the pig, we shall next attempt to determine their significance.

C. Significance of the Variations Observed.

The objections to explaining polydactylism in the pig by the theory of reversion are based on anatomical, embryological, and palaeontological evidence. They have been well summed up by Gegenbaur (**'80**): (1) the accessory pollex is composed of three phalanges, whereas, if due to reversion, it should consist of only two; (2) the other parts of the manus show no modifications toward ancestral conditions; (3) no fundament of the pollex is present at any stage in the embryo pig, nor is it present as a rudiment in any artiodactyle, living or extinct. Gegenbaur, accordingly, concludes that the extra digit is not produced by the development of a vestige, but can be formed only from the duplication of one of the normal digits. Are these objections and Gegenbaur's theory supported by the cases which we have examined?

First, as to the number of phalanges in digit I: in five of our cases there was present a pollex of two phalanges. In the remaining twenty-nine cases, however, there were three elements in each of the extra digits. Gegenbaur is thus right in the main, but there are a few instances which contradict his sweeping statement.

As regards the modification of the other parts of the polydactyle manus, Gegenbaur is again correct in his general statement. But we have seen that in a limited number of cases there are found the identical conditions which he maintains never exist. The trapezium, trapezoid, and third metacarpal of the polydactyle manus resemble in structure the same elements in the manus of certain fossil swine (Ancodus, Palaeochoerus). But the trochlear ridge is found at the distal articular face of the metacarpals in all polydactyle conditions, although it is partly or completely wanting in fossil forms. Other peculiarities of the phalanges of fossil forms are not reverted to.

The musculature also shows some interesting changes. Extensor metacarpi obliquus is in many cases inserted into the metacarpal of the extra digit (I) rather than into metacarpal II. But we know that in the polydactyle manus of man tendons may shift from normal to abnormal digits, although reversion plays no part in producing these abnormalities. The development (1) of the extensor proprius pollicis et indicis (which is rudimentary in the normal manus) and (2) of an independent tendon from the radial side of the flexor perforans are the best evidences presented by the musculature that the extra digit is produced from a vestige. But no great weight can be placed on the structure of the muscles, as their modifications appear to be chiefly adaptive. They are most highly developed when the extra digits are functional, and often to an abnormal degree.

Much greater stress can be laid on the innervation of the polydactyle manus, for the structural conditions are singularly uniform throughout this polydactyle series. In all cases the supernumerary parts are innervated by an independent nerve arising from the radial side of the median trunk, and at about the position where the nerve of the pollex is normally given off in pentadactyle animals. When two extra digits are present in the manus, this branch bifurcates and supplies both. Thus modifications exist in the skeletal, muscular, and nervous organs of the polydactyle manus; they point towards the *vestigial origin of the extra digits, but there is little evidence of reversion in other parts of the manus.*

Gegenbaur's third objection, that the pollex is absent in the embryo and in all adult Artiodactyla, is well taken. For if these are facts, reversion would have to produce a digit of which there is no fundament in the embryo, and reproduce an organ characteristic of only extremely remote ancestors. But Scott ('95) has shown in his work on the American Anthracotheridae, that Ancodus brachyrhynchus has the pollex well developed. We do not, therefore, have to go back further than the Suinae to find a pentadactyle form. As to the absence of the fundament of the pollex in the pig embryo, I have confirmed Rosenberg's ('73) results by examining the carpus of a large number of embryos in various stages of development. For this material I am indebted to Prof. E. L. Mark. There was absolutely no evidence of a pollex-fundament other than the trapezium. This element is generally regarded as being simply the carpal element of digit I, for it develops as a single cartilage. We know, however, that the scaphoid and unciform bones develop in the same way, yet that each represents *two* carpals fused. A careful study of the trapezium in the embryo, in the normal adult and in the polydactyle pig, furnishes some evidence in support of the view that the so-called trapezium represents a rudiment of the pollex as well as a carpal element. (1) In the earliest stages of its development, the cartilage which is to form the trapezium has the pointed distal end characteristic of its adult condition, *and projects distad to the proximal limit of the metacarpus.* (2) In the normal adult carpus the trapezium has always the form of an elongated cone. Its distal end is free, and pointed, instead of truncated, as we should expect if we had to do with only a carpal element. Furthermore, its free end projects farther distad than the other carpal bones and *into the region of the metacarpus.* (3) In the polydactyle manus one case was described in which only the distal end of metacarpal I was developed; yet the so-called trapezium is abnormally long and projects well down by the side of metacarpal II. In three cases where the pollex is developed in a rudimentary condition the *trapezium is fused to metacarpal* I.

In other animals, such as the horse and ox, where there are well-authenticated cases of vestigial polydactylism, the extra digits usually represent the development of rudiments normally present in the embryo. In the case of polydactyle swine, where the extra digits constantly make their appearance in the region of digital reduction, it is but natural to conclude that a rudiment of this digit, even though extremely vestigial, is present in the embryonic manus.

In cases where two (rarely three) extra digits are found in the polydactyle manus, there are no modifications in the other parts. Moreover, it is out of the question to consider digit I^a as representing a prae-pollex and I^b a pollex. Granting that the prae-pollex existed, there are still insurmountable difficulties in the way of this interpretation. Both extra digits develop on a single carpal element, the trapezium. They are supplied by bifurcations of the same muscle tendon, innervated by the divisions of the same nerve-branch, and may even be enclosed distally in the same hoof. In addition, they are usually of the same size and symmetrical with each other. Thus their structure, and the fact that conditions exist intermediate between a single undivided digit and two completely separate ones, make it almost certain that the two extra digits arise from the duplication of the pollex.

Having found good evidence in favor of the vestigial origin of the extra digits, and that Gegenbaur's objections do not hold for all cases, let us examine the evidence in favor of his theory that all cases of polydactylism in the pig are due to duplication of the second digit.

On examining the structure of two digits which are known to be duplications of a single one, we find that they are of nearly the same size, symmetrical with each other, often enclosed in the same hoof, and borne always on a single duplicated carpal element. They are supplied also by duplications of the same muscle tendons, and innervated by the bifurcations of the same nerve-branch.

In the polydactyle cases which we have examined these are not the characteristic conditions. As we have seen, digits I and II always differ greatly in size, often in number of phalanges, and are not bilaterally symmetrical. Digit I is never borne on the trapezoid, but on its own proper carpal, the trapezium; when the trapezium is apparently absent, it is really fused to metacarpal I, or to the trapezoid. The muscular attachments and the innervation of the extra digit are entirely distinct from those supplying and innervating digit II. We can only conclude, therefore, that in these cases the supernumerary digit is not a duplication of digit II. If it were such a duplication, why should not the fifth digit be affected as often as the second? On the contrary, *in every polydactyle manus so far observed the supernumerary digit is found on the radial side of digit* II.

There is no doubt that abnormalities due to the duplication of a functional digit may occur in the manus of the pig as in other mammals; but in the majority of cases the origin of the extra digit must be vestigial. By variation and duplication of this vestige in its development, two or more supernumerary digits may be formed. Whether or not the development of this digital vestige is due to reversion, we will discuss in the theoretical portion of this paper.

Summing up the facts obtained as to polydactylism in the pig, it is found that —

1. Polydactylism is confined almost entirely to the manus. (This fact is interesting, as the condition restores that found in fossil swine. In the pes of Ancodus the hallux is entirely gone, although in the manus the pollex is well developed. If we regard the extra digit as due to duplication of digit II we should expect this duplication to occur as often in the pes as in the manus; but if the extra digit is vestigial in its origin, the early and complete reduction of the hallux in fossil swine is good reason for its never being developed in the pig of the present day.)

2. The supernumerary digits in every case occur on the radial side of the second normal digit.

3. In nineteen of the thirty-six cases examined, a single supernumerary digit is present; in five instances this digit is composed of two phalanges; in nine cases, of three; and in five instances its metacarpal is fused to that of digit II.

4. In the remaining seventeen specimens thirteen are hexadactyle, although in three cases the metacarpal of one supernumerary digit (I^b) is fused to that of digit II; in three instances two supernumerary digits are present, but digit II is entirely wanting; and in one specimen there are evidences of three extra digits.

5. In more than a third of the cases examined, the skeletal, muscular, and nervous organs of the manus give some evidence that the extra digit is vestigial.

6. The trapezium (so-called) may represent this carpal element plus the rudiment of digit I.

7. The extra digits articulate with the trapezium in nearly every case; they therefore represent the development of a vestigial pollex, but may vary extremely from the normal pollex structure.

8. There may be cases where the extra digit is formed by the duplication of digit II, but there is strong evidence against this being the general rule.

9. Two supernumerary digits may be formed by the duplication of the vestigial pollex; there are no grounds for considering one of them a "prae-pollex."

VI. Polydactylism in Ruminants.

A. LITERATURE.

Observations have been made on polydactylism in ruminants and descriptions given by Geoffroy St. Hilaire (**'32–37**), Goodman (**'68**), Chauveau et Arloing (**'79**), Boas (**'90**), Baumüller (**'92**), Blanc (**'93**), and Bateson (**'94**). In the normal manus of ruminants, III and IV are the functional digits, and in all forms save the water chevrotain their metacarpals are fused to form a single "cannon bone." The pollex is always wanting; digits II and V are reduced in varying degrees in the different groups of ruminants. In the camel they are wanting; in the ox metacarpal V remains as a proximal rudiment; the phalanges are completely gone, but a "dew-claw" represents each hoof. The sheep has the two distal phalanges and hoofs of II and V persistent, while in the Cervidae these digits are represented by three well-developed phalanges and the distal ends of the metacarpal bones; the hoofs of digits II and V are functional when the deer is running or travelling over soft ground. In the water chevrotain there are four complete digits, each formed of a distinct metacarpal and three phalanges.

I know of no instance of polydactylism in the camel, and there are few descriptions of such abnormalities in sheep. Geoffroy St. Hilaire (**'32–37**) describes the manus of a lamb in which digits I, II, and V were developed; digits I and II were borne on the same metacarpal and probably represent a duplicated condition of digit II. The best description of polydactylism in the sheep is that of Chauveau et Arloing (**'79**). The manus of a lamb is figured, in which both the second and fifth digits are developed, each being composed of a distinct metacarpal element and three phalanges nearly as large as those of the functional digits. This condition is certainly due to the development of vestiges, and has been attributed to reversion.

Baumüller (**'92**) figures the manus of a roebuck (Cervus caprea) which was composed of five digits. The abnormality was found on both fore feet. Baumüller regards the extra digit as a pollex, and attributes its presence to reversion.

Bateson (**'94**) remarks with reference to polydactylism in the sheep and ox, that the extra digits are in all cases formed by duplication or variation. As to the development of digits II and V he asserts that "there is no such case."

In the ox, a number of cases of polydactylism have been observed and described. They may be divided into two groups: (1) manus or pes of three digits, all of nearly equal size, and borne on a single metacarpal bone (Bateson, **'94**, Figs. 114, 115, p. 375). In these cases the presence of both accessory hoofs (rudiments of II and V) in their normal positions makes it certain that the vestiges of digits II or V have not developed, but that either III or IV has become duplicated. Four cases are described by Bateson, and it is stated by Goodman (**'68**) that the abnormality was common and frequently inherited in a herd of English cattle. (2) Manus of four digits, II and V both being developed; the accessory hoofs are located at the distal extremities of the extra digits; each supernumerary digit is composed of a distinct metacarpal element, and digit II has in addition two small phalanges. Boas (**'90**) describes two cases, and considers them good instances of reversionary polydactylism.

B. Observations.

Two cases of polydactylism in the manus of the ox have come under my observation. Both specimens had been disarticulated at the carpo-metacarpal joint, and the carpal bones were thus unfortunately lost; they were right and left fore feet and probably belonged to one animal. Both are abnormally wide at the distal end of the cannon bone; in each the hoof of the radial side is very broad and incompletely divided into two parts (Fig. *W*, p. 294, and Plate **21**, Fig. 29). The accessory hoof of the ulnar side of the manus is normal in position, but that of the radial side is absent in both cases.

In the left manus (Fig. 29) the skeletal parts are well formed. The metacarpus is of normal length, and is distinctly divided into three elements, each of which bears an articular head for a corresponding digit. These three elements represent three metacarpal bones, and we may designate them as II, III, and IV. III is larger than either of the others; its distal articular surface is unsymmetrical, as the trochlear ridge has shifted toward the ulnar side. The supernumerary metacarpal (II) is the smallest of the three; it is fused to III throughout its whole length, and can be traced to the proximal extremity of the metacarpus, where it takes part in forming the articular facet for the carpals. The distal epiphysis extends beyond those of the normal metacarpals, has a flattened instead of a convex articular surface, and no trochlear ridge. The fifth metacarpal (Fig. *W*, V) is, as normally, a rudimentary stylet articulating at the ulnar side of the proximal extremity of IV.

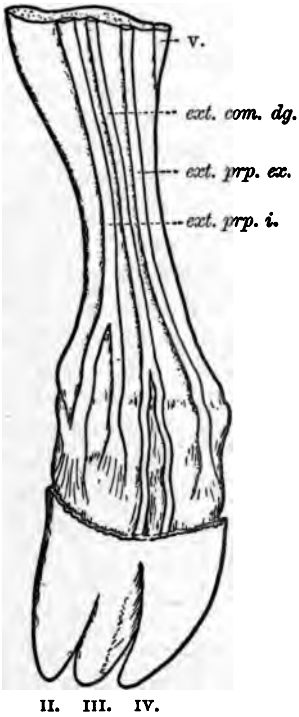

FIG. *W*. — Anterior view of the left polydactyle manus of a calf, showing the extensor muscles. II, supernumerary digit; V, metacarpal of digit five; *ext. com. dg.*, extensor communis digitorum; *ext. prp. ex.*, extensor proprius externus; *ext. prp. i.*, extensor proprius internus. ½ natural size.

All three digits are composed of three phalanges. Digit IV is apparently normal; digit III is more massive, and the symmetry of its phalanges and hoof is affected by the presence of the abnormal digit. Instead of being optical images of those of digit IV, these bones are indifferent in their conformation, curving neither to the right nor to the left. The hoof in which the ungual phalanx is enclosed is common also to digit II. The extra digit (II) is shorter and not so massive as the normal ones; its ungual phalanx is flattened laterally, and more pointed than the normal phalanges; the sesamoids are absent.

Dissection of the musculature of this manus shows that the flexors are entirely normal; the extensors, however, exhibit an important modification. The tendon of the extensor proprius internus (Fig. *W*, *ext. prp. i.*) divides, and the more radial of the two slips thus formed is inserted into the second and ungual phalanges of the supernumerary digit. Before its insertion this tendon is joined by a division of the suspensory ligament. The anatomical relations of this tendon thus resemble the normal condition in four-toed animals. If the supernumerary digit is a duplication of digit III, we should expect to find the extensor communis digitorum (*ext. com. dg.*) and the flexor tendons bifurcated; but they are unmodified.

The nerves of this manus also show important modifications. The normal manus, like that of swine, is innervated by four branches of the median nerve; the most radial and most ulnar branches (compare Fig. *X*, 2, 5) give off small twigs to the rudiments of digits II and V. Branch 5 is joined by the ulnar nerve immediately before it divides to form 5 *a* and 5 *b*. In the polydactyle manus (Fig. *X*, 2, 5) the modification is in connection with the small fasciculus (2^a), which normally innervates the radial accessory hoof (rudiment of digit II). This is no longer a mere filament ending at the distal end of the metacarpus, but a moderate-sized branch, which continues to the hoof and ungual phalanx of the supernumerary digit. The condition of this nerve branch, together with the fact that the accessory hoof of this side is absent, affords most convincing proof that this abnormality is not a monstrosity, or a duplication of digit III, but is due to the development of digit II.

The second case, a right manus, confirms by its structure the conclusion which we have drawn from the first.

The line of demarkation between the second and third metacarpals is even more distinct (Plate **22**, Fig. 30); the first and second phalanges of digit II are fused together and are abnormally short.

Rosenberg (**'73**) states that metacarpals II and V are present in the embryo of the sheep and ox, but later partially degenerate and fuse to the cannon bone, a small portion of V remaining distinct in the ox. In the Cervidae the distal ends of the metacarpals persist in the adult. It is not surprising therefore that we find these digital rudiments occasionally developed in the adult ruminant.

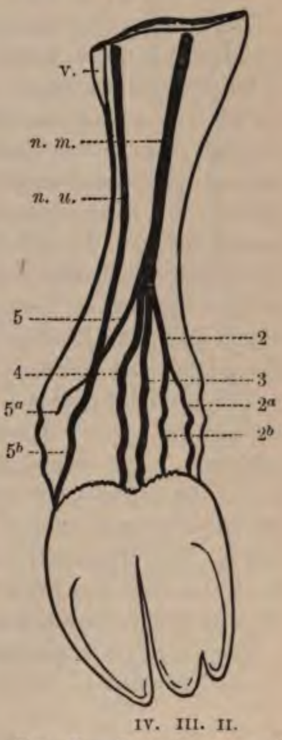

FIG. *X*. — Posterior view of left polydactyle manus of the calf, showing innervation. II, extra digit; V, metacarpal of fifth digit; *n. m.*, median nerve; *n. u.*, ulnar nerve; 2–5, four branches of median nerve; 2^a, division of second branch which supplies the extra digit (II); 5^a, division of fifth branch which innervates the accessory hoof (digit V). ½ natural size.

Polydactylism in ruminants is thus of two types: (1) vestigial, due to the development of either digit II or V (or both); (2) teratological, produced by the duplication of one of the functional digits (III or IV).

VII. Polydactylism in the Equidae.

A. LITERATURE.

The anatomy and diseases of the horse have been studied almost as thoroughly as those of man, and consequently we find that polydactylism in the Equidae has received considerable attention. Aside from the classical allusion of Suetonius ('86) to the horse of Julius Caesar "which had feet that were almost human, the hoofs being cleft like toes," the first account of polydactylism is that of Winter (1703), who describes two cases. Geoffroy St. Hilaire ('32–37) records a foetus which was polydactyle in the fore feet, the left foot bearing three nearly equal digits, and the right two. Numerous instances have since been noted, the more important descriptions being those of Arloing ('67), Wood-Mason ('71), Marsh ('79, '92), Ercolani ('81), Boas ('85), Pütz ('89), and Ewart ('94). Blanc ('93), and Bateson ('94) review the general subject.

The normal functional digit of the Equidae is III of the typical mammalian manus; it consists of a long metacarpal bone and three phalanges. The ungual phalanx is completely enclosed in a massive hoof. Two splints, representing the metacarpals of digits II and IV, articulate at each side of the cannon bone posteriorly and with the carpus. The trapezium is a small pea-shaped rudiment lying posterior to the trapezoid and often wanting. The os magnum is very large, and with it, chiefly, the cannon bone articulates.

The polydactyle cases cited by various investigators fall into two groups, the first of which may be subdivided into three:

(1) *Supernumerary digits representing the development of digital vestiges.*

a. Three metacarpals, the extra digits being borne on II *and* IV. The condition of an extra digit borne on metacarpal II may occur on all four feet (Marsh, '92) or be limited to the manus (Arloing, '67). The extra digits are always smaller than III and do not function in locomotion; this condition is of quite frequent occurrence. A single case is cited by Wood-Mason ('71), in which an extra digit of three phalanges occurs on metacarpal IV; the radial splint bone (II) was also somewhat better developed than in a normal manus. Cases of three digits (both II and IV being developed) are cited by Geoffroy St. Hilaire ('32–37) and Marsh ('92), but no good anatomical descriptions are given.

b. Four metacarpals; digit I is represented by a splint radial to digit II, which is fully developed and composed of three phalanges (Fig. *Y*).

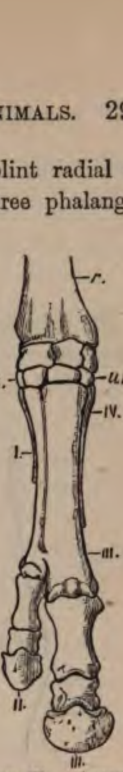

FIG. *Y*. — Anterior view of left polydactyle manus of horse. I, metacarpal of first supernumerary digit (pollex); II, second supernumerary digit; III, functional digit; IV, metacarpal (splint) of fourth digit; *r*, radius; *trz.*, trapezium; *un.*, unciform. (After Marsh.)

In these cases there are four large bones present in the distal row of carpals. Digit II is large, and its metacarpal is fused throughout most of its length to that of digit III. Four cases are cited by Marsh ('92), and one is carefully described by Bateson ('94).

A different interpretation from that here assumed may be brought forward in explanation of these cases. The digit designated as II in Figure *Y* may be regarded as a duplication of digit III, and the so-called trapezoid of the carpus may represent a duplication of the os magnum. Then the bone designated as trapezium must be the true trapezoid, and its splint bone the second, not the first, metacarpal. Only by a careful examination of the skeletal, muscular, and nervous structures can we determine which interpretation is correct; whether digit II is of vestigial origin, or due to a duplication of digit III. The fact that in phylogeny the pollex disappeared long before the fifth digit is a strong argument against the former interpretation. For by that interpretation we should here have the pollex reappearing, and the second digit almost as large as the third, while the fourth digit is unmodified and the fifth is entirely absent.

c. Five metacarpals; one supernumerary digit, borne on metacarpal II. One case is described by Pütz ('89) in which the trapezoid bears digit II; this consists of a well-developed metacarpal bone and three phalanges. Radial to this is a large trapezium, articulating with the scaphoid and trapezoid and bearing a splint six cm. long; metacarpal IV is normal, and on its ulnar side is another metacarpal element supposed to represent digit V. The supernumerary elements in this case can only be explained as of vestigial origin.

(2) *Two digits borne on metacarpal* III.

These are clear cases of duplication, and have been described in the manus only. The doubling may extend to the metacarpal bone, but is usually limited to the phalanges. Such conditions have been described by Struthers ('**63**), Arloing ('**67**), and Boas ('**85**).

B. Observations.

Through the kindness of Dr. Frothingham, of the Harvard Veterinary School, an abnormal manus of a polydactyle colt came under my observation. The specimen came from Texas. Externally the hoof was almost completely divided into two; each portion was several inches long, and curved away from the other. On examining the skeletal parts (Fig. *Z*), they were found to be normal down to the distal end of the first phalanx, which was bifurcated and bore two articular surfaces. Each of these carried two phalanges, which resembled the median and ungual phalanges of the artiodactyle digit. The two series were mirrored images of each other; each os pedis was slightly concave on the surface facing the median plane of the digit, and convex on the opposite side, so that the two fitted together would give a phalanx of nearly normal form. A navicular of about half the length of the normal bone articulated with the posterior face of each os pedis, thus resembling the condition of ruminants.

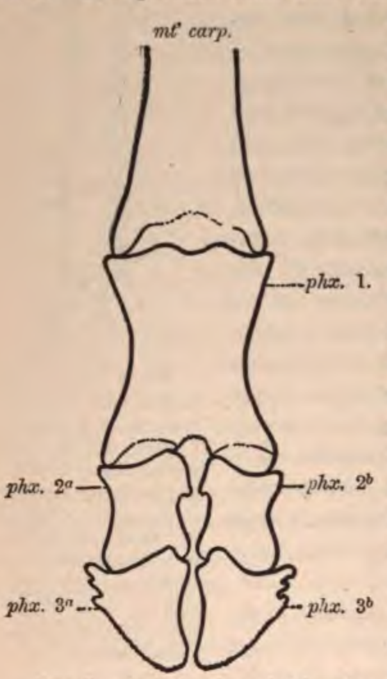

Fig. *Z.* — Anterior view of left polydactyle manus of the horse, showing duplication of digit III. *mt' carp.*, distal end of third metacarpal bone; *phx.* 1, first phalanx of third digit; *phx.* 2^a, 2^b, duplications of second phalanx; *phx.* 3^a, 3^b, duplications of ungual phalanx. ⅓ natural size.

This specimen had been dried before it was examined, and the innervation could not be studied, but examination of the chief muscle tendons showed that the extensor pedis and flexor perforans were duplicated at their distal ends. This case is therefore simply an example of duplication of digit III.

It has long been known that the "splint bones" of the equine manus represent rudimentary metacarpals, but until recently the presence of phalangeal vestiges in the manus of the embryo has been denied.

Rosenberg (**'73**) searched for such vestiges, but without success. Ewart (**'94**), in tracing out the skeletal development of the limbs of the horse, found cartilaginous nodules articulating in an imperfect manner with the distal epiphyses of metacarpals II and IV. The vestige attached to digit II was the larger, and in some instances showed evidence of division into two or three parts, which Ewart takes to be the fundaments of as many phalanges.

This is an interesting and important discovery, since, if digit II is better developed than IV in the normal embryo, we have a good explanation for the fact that in polydactyle horses it is the second digit which is of most frequent occurrence. Dissection of the manus of a foetus 35 cm. long enabled me to confirm Ewart's work. There is thus conclusive evidence that in the horse extra digits are frequently of vestigial origin. The digital abnormalities of the Equidae can therefore be divided into two distinct classes:

(1) Vestigial cases, in which the extra digits are developed from rudiments normally present in the manus of equine embryos and extinct ancestors.

(2) Teratological cases, which are malformations usually due to the partial or complete duplication of the functional digit (III).

VIII. Theories of Polydactylism.

The occurrence of polydactylism has been attributed to two proximate causes: (1) External influences, (2) Internal influences.

1. EXTERNAL INFLUENCES.

The supporters of this theory (Ahlfeld, **'85–86**, and Zander, **'91**) would explain all cases of digital variation as due to the pressure of amniotic threads *in utero.* This view accounts satisfactorily for the variation in degree of digital duplications, but utterly fails to explain their fixed position with reference to certain digits, and cannot apply to the development of digital vestiges. Pressure from an amniotic thread would naturally affect *any* finger or toe, whereas we know that polydactylism in mammals is practically limited to the first or fifth digit, is often bilaterally symmetrical in its occurrence, and may affect both manus and pes in the same individual. The abnormalities are also strongly inherited, and the amniotic theory, if correct, would necessitate admitting the inheritance of acquired characters. Although the duplication of organs has been artificially produced by Dareste (**'91**) and others, it has yet to be proved that such modifications are inherited. Certain cases of digital duplication are undoubtedly caused by the pressure of amniotic threads. Such abnormalities are true malformations, and usually affect a normal, unreduced digit. An assured case is that of a duplicated thumb described by Ahlfeld, in which a fold of the amnion was found at birth still adherent between the duplications of the pollex. It is possible that certain cases where a single functional digit is duplicated are produced in a similar manner. Such examples of polydactylism, however, are the exceptions rather than the rule, for in both mammals and birds we have seen that the typical, unmodified, functional digits vary but rarely. Under this class might come the cases of partial or complete duplication of digits II–IV in birds and man; of digits II–V in carnivores; of digits III and IV in artiodactyles, and of digit III in the horse. Some cases of the duplication of digits I and V in man and of digits II and V in swine may also be included in the above category; but it may be that all the symmetrically placed, hereditary digital abnormalities are produced by some internal influence emanating from the germ itself.

2. INTERNAL INFLUENCES.

One of the most important facts brought out by the comparative study of polydactylism is its limitation chiefly to the *variation of digits which normally are either modified, rudimentary, or vestigial.* It is natural to conclude that all such variations are due to one and the same cause. But on comparing the different types we find that it is only in the horse, ruminants, swine, and the pes of carnivores that extra digits arise as *vestigial* developments; whereas, in man, the fowl, and the manus of the cat they are formed as *duplications of functional digits.*

a. Reversion.

The theory of reversion, first proposed by Darwin to account for polydactylism in man, has been supported, and extended to all mammalian forms, by Bardeleben ('85), Albrecht ('86), Kollman ('88), Cowper ('89), and Blanc ('93). Boas ('85, '90) limits reversionary polydactylism to the horse and ox. Marsh ('92) asserts that the digital variations in the Equidae can be accounted for in no other way. Gegenbaur ('80, '88), while strongly opposed to the theory in general, admits that it may be applicable to polydactylism in the horse.

Reversion, as generally understood, is but heredity carried to an extreme in point of time. It is the inheritance by an individual of qualities peculiar to a distant ancestor, — qualities which were once characteristic of the species, but have been lost in the evolution of varieties. Consequently, the best-authenticated instances of reversion are those in which individuals of a certain variety or breed return to the characters of the original species. Well-known examples are the reversion of domestic varieties to the character of the wild rock-pigeon; the recurrence of shoulder-stripes and a dun coloration in the horse and mule; the appearance of longitudinal stripes on the backs of young domestic swine when allowed to return to the feral state, — a coloration peculiar to the sucklings of the wild ancestors of the hog, but normally wanting in the young of the domestic pig. In these cases, which we know are reversionary, it may be observed (1) that the phenomenon is simply the return of individuals of a variety to the original characteristics of the species; (2) that the variation in such reversions relates merely to the degree of completeness with which the atavistic qualities are transmitted; monstrous conditions, or malformations, are never thus produced.

In animals in which the typical number of functional digits is normally reduced (pes of Carnivora, swine, ruminants, and Equidae), the supernumerary digits in the majority of cases are developed independently of the normal digits, but in connection with embryonic vestiges or rudiments. Is not reversion, then, the factor which is operative here, causing the development of degenerate digits, and thus tending to restore the original pentadactyle condition? The objection is raised, however, that there is *too great a distance in point of time and relationship between the polydactyle animal and the pentadactyle ancestor to which it is supposed to revert.* According to the old idea of heredity this might seem true, but in the light of Mendel's law (recently fully confirmed) it is no longer a serious objection. As pointed out by Bateson and Saunders (:**02**) and Castle (:**03**), the important facts discovered by Mendel are that a single parental character may be segregated in the *germ-cells* of the offspring, and that *one* of a pair of parental characters may regularly dominate over the other; further that each of the offspring, though exhibiting the dominant character only, produces ripe germ-cells half of which bear the dominant character of one parent, the other half, the recessive character of the other parent. Thus, if the polydactylous Dorking is crossed with the normal Leghorn, nearly all of the hybrids will be polydactylous — not quite all, however, for the extra toe in this case is not completely dominant. But continued breeding shows that the sperm and ova of the crossbreds will bear either the dominant polydactylous character, *D*, or the normal recessive character, *R*, and that equal numbers of *D*'s and *R*'s will be produced. Offspring of the crossbreds will therefore show these characters in the following ratios:— 1 *D* : 2 *DR* : 1 *R*. But the character *D* being dominant, not only the 1 *D*'s but the 2 *DR*'s will be polydactylous and therefore only one-fourth of the chicks will have normal toes. Bateson's experiments show that this is really the case.

To us the significance of Mendel's law lies in the fact that a certain character may be transmitted pure from generation to generation of germ-cells in a latent condition; that is, the character may not appear in the structure of the animal, though present in its germ-cells.

The occurrence in a latent condition of characters which when active are dominant may thus explain the constant outcropping of these characters, such, for example, as the continual appearance of "rogues," in apparently pure races of plants and in animals which have been selectively bred for generations. The appearance of reversionary polydactylism may be explained in this way.

Although we know that in the horse, ruminants, swine, and the pes of carnivores the extra digits may be of vestigial origin, yet Gegenbaur has objected that there is no other evidence of reversion, either in the polydactyle extremity or in the general appearance of polydactyle animals.

We have shown that in polydactyle swine the abnormality is confined to the manus, and that in most, if not all, cases the extra digits represent the development of the normally vestigial pollex. In a third of the cases a well-formed digit of two or three phalanges is found, and when these conditions are compared with those of the manus of the earliest fossil swine, it appears that the two are similar; for a pollex is found in the manus of the fossil pig, while in the pes the hallux is entirely wanting. In addition to the development of the pollex, other modifications were found in the structure of the polydactyle manus, which seemed to reproduce a primitive, ancestral condition. We have also seen that in most cases of polydactylism in the ox and horse the extra digits represent the development of digital parts normally rudimentary, — a development which might be regarded as due to reversion, for other parts of the polydactyle member show correlated variations, and related fossil ancestors also have the same digits normally developed and functional. Moreover, according to recent discoveries in heredity, single segregated characters may be inherited, without general modification of the germ-plasm. This has been proved by Bateson and Saunders (:02), Castle (:03, :03^{a}) and others in agreement with Mendel's law.

The least answerable of the arguments against the general occurrence of reversionary polydactylism is the fact that more than five digits are found in certain cases of polydactylism (man and cat), and that in other cases the extra digits, though of vestigial origin, are exceedingly variable, and often duplicated (swine and pes of Carnivora). Some factor other than reversion must enter here, unless we assume with Albrecht ('86) that the tendency to digital duplication is reversion to the bifid fin-rays of elasmobranch fishes, or with Bardeleben ('86) that the sixth and seventh digits represent reversions to a hypothetical six-toed or seven-toed ancestor. Albrecht's assumption seems absurd, for we know that such duplications are of common occurrence in the development of other structures to which his explanation of reversion cannot apply. Likewise, it has been clearly shown by various investigators that Bardeleben's "prae-pollex" theory is a mere assumption unsupported by the evidences of anatomy, embryology, or palaeontology. For (1) the "prae-pollex" rudiments never develop into digits and are not located in the region where the supernumerary digits appear in man (Förster, '61; Gegenbaur, '88; Zander, '91). (2) They are not the vestigial remains of a degenerating digit, but secondary developments, or neomorphs (Tornier, '89; Carlsson, '90; Wiedersheim, :02). (3) The most primitive reptilian fossils (the Ichthyopterygia) possess only five digits (Baur, '87). The "prae-pollex" theory is thus rightly rejected by such eminent anatomists as Gegenbaur and Wiedersheim. With it, as a consequence, must go the assumption that polydactylism in pentadactyle extremities is a reversion to a heptadactyle type.

In comparing the skeletal parts of the polydactylous manus shown in Figure 13 (Plate 5) and in Figure *K* with the normal and fossil conditions (Figs. *F* and *G*), no one can doubt that reversion is the true cause of such abnormalities. The same conclusion holds true for a fully formed hallux in the dog and for the cases of vestigial polydactylism in the horse and ruminants. It seems probable, however, from the variations which we have described in swine, that the character of digits produced by reversion is not firmly fixed in the germ, and that on crossing with normal animals, the abnormal character, since it is dominant in Mendel's sense of the word, is transmitted to the offspring, but in different degrees of variation and duplication. Experimental breeding may settle this question, but at present we can only argue from analogy with other forms. Thus, Bateson found that the extra digits of the fowl varied greatly on crossbreeding. But in the case of the fowl the extra digits are sports, not palingenetic structures.

We have suggested the possibility that a factor in the production of polydactylism in man, the cat, and the fowl may be reversion, ***not*** to a hypothetical heptadactyle ancestor, but to the unmodified minimus, pollex or hallux of a not distantly related pentadactyle form. The re-acquired structures might prove to be in their germinal characters, like those of many neomorphs, so unstable as to lead to variations in the next generation, such as polydactylous duplications.

We have evidence to show that in man, the cat, and the fowl it is ***not a definite number of extra digits, but a tendency to digital variation and duplication*** which is inherited. In man the minimus may be duplicated on all extremities, but to a different degree in each case, and the variations may increase in succeeding generations. Thus, Fackenheim ('**88**) cites the case of normal parents whose daughter had a rudimentary sixth finger on the ulnar side of each hand. Of her two sons, one had six fully developed digits on each hand, the other six digits ***on all four extremities!*** In another family the first parent observed had six toes on each foot. Of eight children three were normal, three had six toes (in one case correlated with hare-lip), and two had six fingers; all the extra digits were of symmetrical occurrence. In the three succeeding generations extra digits appeared ***now on the feet, now on the hands,*** and in two cases ***on all four extremities.*** In two cases also, ***seven toes*** were present on one or both feet.

In a family of cats observed by Poulton ('**86**) the abnormality appeared in the third generation (number of extra digits not stated). In the fourth generation six toes appeared on all four extremities. In the fifth generation there ***were many individuals with seven*** toes on all paws, and evidences of further duplication in the existence of doubled claws. All gradations occurred between the extreme and normal form. This condition prevailed up to the ninth generation, although in every case the male parent was normal.

Torrey (:**02**) describes a similar case in which the offspring of a female cat with six toes on the manus and five on the pes showed all gradations between the normal and a seven-toed condition. Often in these cats the pollex was ***abnormally long and composed of three phalanges*** instead of two. In all cases digits II–V were apparently normal in structure.

Bateson's breeding experiments show the same to be the case in the polydactylous fowl. On crossing with normal birds all degrees of variation are exhibited by the hallux, from simple elongation to complete duplications and reduplications.

These observations bring out the important fact that often ***no extra*** *digit is produced,* but simply a *variation in the structure of the pollex, hallux, and minimus.* It would seem, therefore, that it is this tendency of the modified digits to vary which is inherited.

We know that such digital variations occur also in the offspring of normal individuals, and that they are inherited. Bateson cites the occurrence of such a case in cattle and the formation of a three-toed race thereby. The duplication of appendages is common in the lower animals, and variation is of frequent occurrence in all neomorphic organs. Well-known examples are the duplicated claws of arthropods and the doubled horns of sheep. Polydactylism according to Fackenheim (**'88**) is often correlated with abnormality by defect.

None of these variations can be attributed to reversion. The law of Mendel, as Bateson and Saunders (**:02**, p. 150) have pointed out, "applies only to the manner of transmission of a character already existing. It makes no suggestion as to the manner in which such a character came into existence." Bateson regards the polydactyle fowl as "a palpable sport;" the usual digital abnormalities of the fowl, the cat, and of man undoubtedly belong to the same class of polydactylous abnormalities. It is possible that reversion may be the *primal* cause in producing certain of these digital variations, but the present evidence does not warrant a positive statement to that effect.

b. Germinal Variation.

This has been regarded as the chief factor in polydactylism by Förster (**'61**), Darwin (**'76**), Gegenbaur (**'80**), Howes (**'92**), Weismann (**'93**), Bateson (**'94**), Wilson (**'96**), and many others. Weismann's view (**'93**, p. 329) is, that excessive nutrition in the cells of the embryo may cause the duplication of a group of determinants which are to form a particular digit; the doubled condition of the determinants might then be inherited, and thus the inheritance of these digital abnormalities accounted for. This, however, does not explain the changes in position which digital variations in man may undergo in the course of hereditary transmission (that is, from fingers to toes). Wilson (**'96**) attempts to clear up this point by assuming that there may be variation in those determinants which affect the nutrition of the digital fundament, and that it is the tendency of these determinants to vary which is transmitted, rather than the doubled condition of the digital determinants themselves.

There is some direct evidence that germinal variation is due to an excess of nutrition. It has been observed by Ercolani (**'81**) and Boas (**'85**, **'90**) that certain polydactyle conditions in the ox and horse occurred along with the atrophy, partial or complete, of the functional digits, which apparently caused the subsequent development of the normally rudimentary ones. In these instances it would seem that the nutriment which is normally appropriated by the functional digits is transferred to, and utilized by, the digital rudiments, thus enabling them to continue their development. We are familiar with the same phenomenon in plants, where, if the terminal bud is removed, lateral buds, which would otherwise have remained dormant, are stimulated to development by the extra supply of nutriment which they receive. Again, polydactylism very often accompanies acephalic conditions, and other abnormalities due to defect of some organ, as recorded by Fackenheim and others. Here the same law is applicable; on account of the abnormal absence of certain organic fundaments, the remaining ones receive more than their usual amount of nutrition; as a result, an increased development of normally reduced or otherwise modified digits may be brought about. But these cases of polydactylism may also be explained as due to external influences acting *in utero.* Fackenheim has shown that in a certain family polydactylism did not appear as a correlative of inherited abnormality by defect, until one of its members married into another family in which digital abnormalities were of frequent occurrence. Then only did offspring appear afflicted with both polydactylism and defective teeth. From such cases the evidence that excess of nutriment causes germinal variation loses much of its weight.

Any explanation of the phenomena of germinal variation must necessarily be theoretical, as long as our practical knowledge of the germ-plasm is so limited. We know, however, that all neomorphs are prone to variation. In polydactylism all the digital abnormalities produced by internal causes vary greatly, and the tendency to variation is inherited. By Mendel's law the inheritance of these variations is explained, and the puzzling point which Wilson ('96) attempted to clear up by his theory of nutritive variation, is made plain, — the fact that in man an individual having a polydactyle manus may produce offspring with abnormal pes or with all extremities abnormal. In this case we may assume that the variation first appeared on all extremities as a duplication of the minimus, due to the doubling of the determinants of these digits. On marrying with a normal individual the abnormal character would be dominant, but not completely so (Bateson found this to be the case with the polydactyle fowl). Of the *DR* offspring produced, some would be abnormal like the *D* parent, but in others the usually dominant character might be recessive; their extremities might be entirely normal, or only the hands polydactyle. In either case, however, they would be capable of producing other *DR* offspring, if married to normal individuals, and these offspring might themselves be normal or polydactyle; should they marry with recessive individuals like themselves, pure *D*'s would be produced as well as *RD*'s, and such individuals again would be polydactyle on both hands and feet. Wilson's theory of nutritive variation is thus rendered unnecessary, as Mendel's law explains how all cases of polydactylism, not due to external causes, may be the result of inheritance.

All such inherited types of polydactylism are thus ancestral. But only those forms in which the extra digits develop directly from rudiments and vestiges may be attributed to palingenetic reversion. In those cases in which digital rudiments and vestiges are duplicated, reversion and germinal variation may occur together; but the duplications of functional digits are probably caused by germinal variation alone. As to the cause of these germinal variations, or sports, we know little or nothing.

IX. Summary.

1. Polydactylism consists in an excess in the number of digits possessed by the individual over the number peculiar to the species.

2. The supernumerary digits generally occur symmetrically placed on the right and left extremities, either in the manus, in the pes, or in both; they are found most frequently in the manus.

3. The extra digits are formed most frequently in connection with the fifth and first digit in man; with the first digit in the fowl, Carnivora, and swine; with the second digit in ruminants and the Equidae. In general, *polydactylism may be said to affect digits which are normally much reduced or modified.*

4. Cases of polydactylism in which more than five digits occur cannot be attributed to reversion alone (a heptadactyle ancestor is hypothetical, the so-called prae-pollex and post-minimus are rudiments of secondary development, and they have never been known to produce functional digits).

5. Palingenetic polydactylism is limited to those forms in which — the number of functional digits being normally reduced to fewer than five — the digital rudiments develop and reproduce, more or less completely, the structure of homologous digits typical of some ancestral form. The evidences of comparative anatomy, embryology, and palaeontology show this to be the case in the horse, ruminants, and swine; possibly in the pes of Carnivora.

6. This eventual dominance of a digital character, which has been

transmitted in a recessive condition through many generations, is in strict accordance with Mendel's law of heredity.

7. Neogenetic and palingenetic forms of polydactylism are, like other new characters, extremely variable; as they are hereditary, we may conclude that duplications of both functional and vestigial digits are due to variations in the gametes.

8. The polydactyle abnormalities of man and the domestic animals may be classified as follows:

I. *Teratological polydactylism* includes those cases of digital duplication and malformation which are produced by external influences; it occurs rarely in all animals, often in correlation with other monstrosities.

II. *Neogenetic polydactylism* includes those digital variations, or sports, which are produced by some internal cause, presumably germinal variation.

a. Duplication of *unmodified* functional digits occurs occasionally in all animals and is transmissible.

b. Variation of *modified* but functional digits is the ordinary form of polydactylism in man, the cat, and the fowl (pes), and it also is transmissible.

III. *Palingenetic polydactylism* includes those cases in which digital rudiments, or vestiges, develop into extra digits.

a. The extra digits reproduce more or less completely the structure of the homologous functional digits of related fossil ancestors; this condition is found in the horse, ruminants, swine, and the pes of the dog.

b. The extra digits arise as variations or duplications of rudiments, or vestiges; they are neogenetic in so far as they do not reproduce ancestral conditions. Examples are the hallux and pollex having three phalanges and the various duplications of these digits found in the manus of swine and the pes of Carnivora.

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EXPLANATION OF PLATES.

The figures are all reproduced from natural size skiagraphs of the polydactyle specimens; in every plate the distal ends of the extremities are down, but right and left are reversed. Right extremities therefore appear as left in the figures, and *vice versa*.

ABBREVIATIONS.

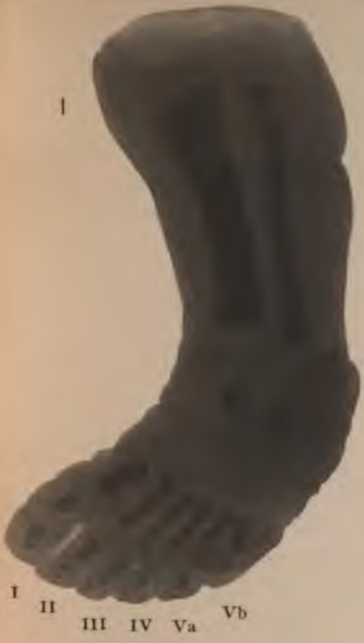
asg.	**Astragalus.**
cac.	Calcaneum.
cub.	Cuboid.
cun.	Cuneiform.
ec'cun.	Ectocuneiform.
en'cun.	Entocuneiform.
ext. com. dg. i.	Extensor communis digitorum internus.
ext. mt'carp. mag.	Extensor metacarpi magnus.
ext. mt'carp. ob.	Extensor metacarpi obliquus.
ext. prp.	Ext. proprius pollicis et indicis.
ext. prp. ex.	Extensor proprius externus.
ext. prp. i.	Extensor proprius internus.
flx. perf.	Flexor perforatus.
flx. perf.'	**Flexor perforans.**
lun.	Lunar.
ms'cun.	Mesocuneiform.
mt'carp.	Metacarpal.
mt'tar.	**Metatarsal.**
nav.	Navicular.
n. m.	Median nerve.
n. uln.	Ulnar nerve.
os. mag.	Os magnum.
phlx.	Phalanx.
pis.	Pisiform.
scph.	Scaphoid.
trz.	Trapezium.
trzd.	Trapezoid.
un.	Unciform.
I–V	First to fifth digits.
1–5	First to fifth branches of the median nerve.

PLATE 1.

All figures are skiagraphs of human appendages.

FIG. 1. Right foot of foetus, No. 6730.
FIG. 2. Left foot of foetus, No. 6730.
FIG. 3. Left hand of foetus, No. 912.
FIG. 4. Right hand of foetus, No. 912.
FIG. 5. Left foot of foetus, No. 912.
FIG. 6. Right foot of foetus, No. 912.

1



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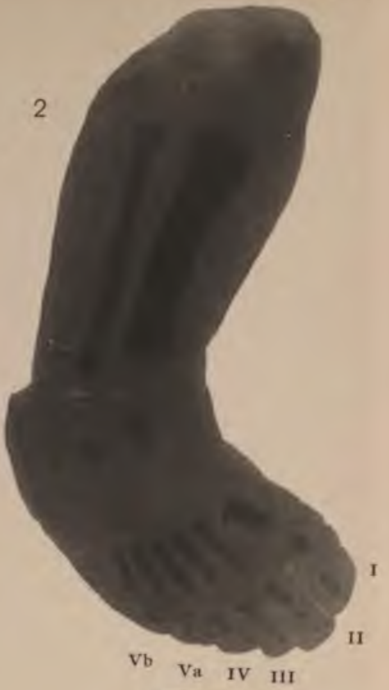

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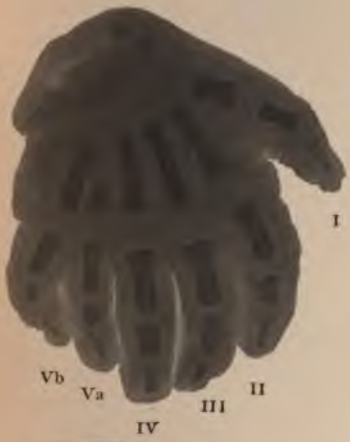

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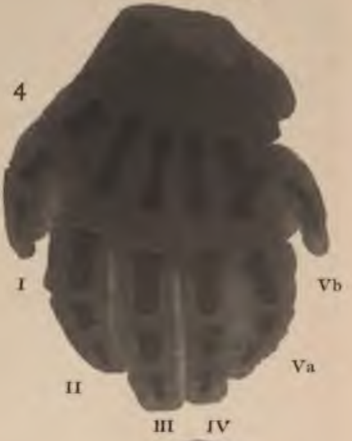

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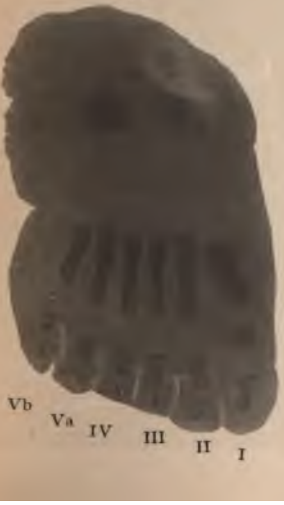

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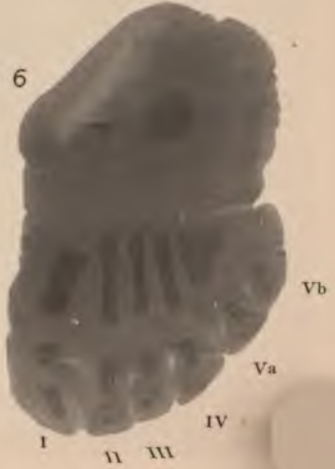

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PLATE 2.

All figures are from skiagraphs of human foetal appendages.

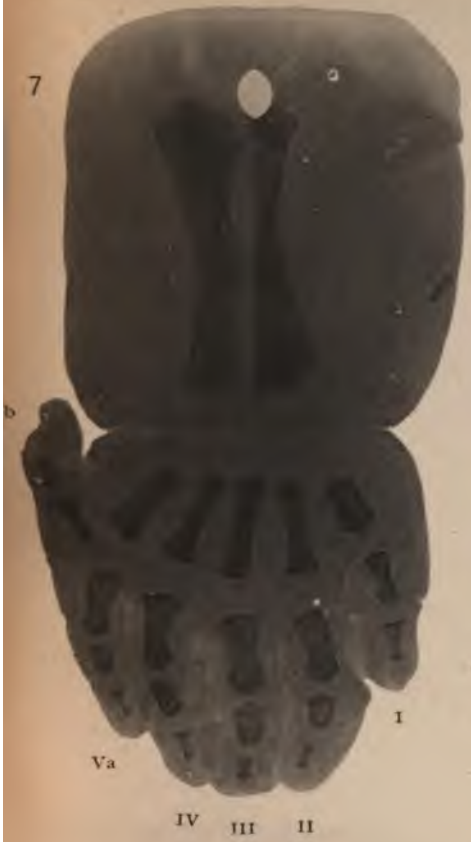
FIG. 7. Left hand of foetus, No. 5809.

FIG. 8. Right hand of foetus, No. 5809. NOTE. — The metacarpal mentioned
the text (p. 254) has failed of reproduction in the printing of this pl

FIG. 9. Right hand of foetus, No. 913.

FIG. 10. Left foot of foetus, No. 913.

7



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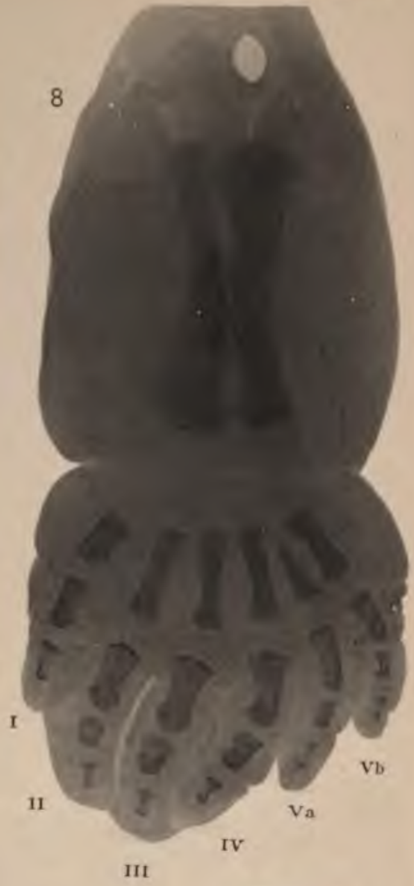

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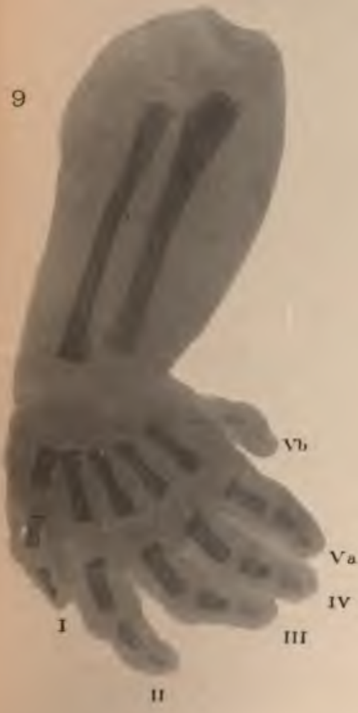

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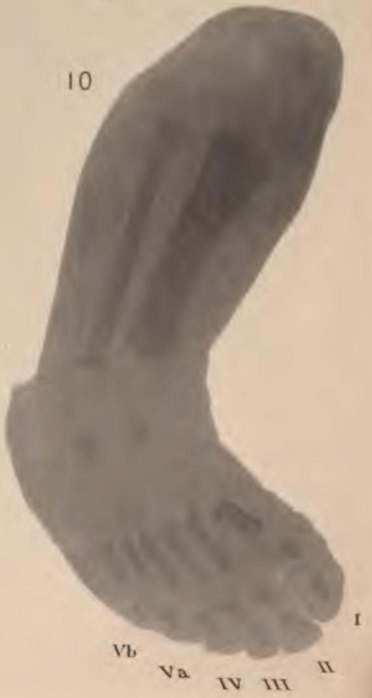

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PLATE 3.

FIG. 11. Normal left manus of the pig, anterior view, showing skeletal structure of the digits.

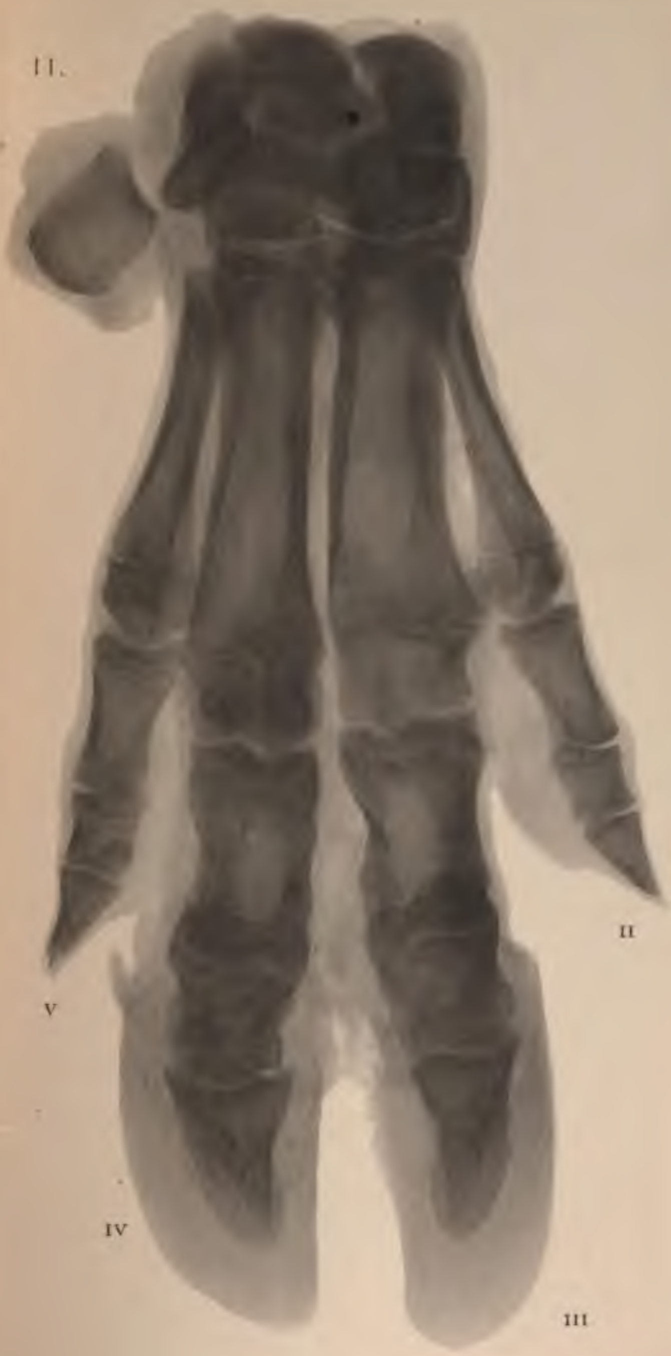

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PLATE 4.

FIG. 12. Anterior view of left polydactyle manus of the pig, showing a small supernumerary digit (I) and the lower row of carpals.

12

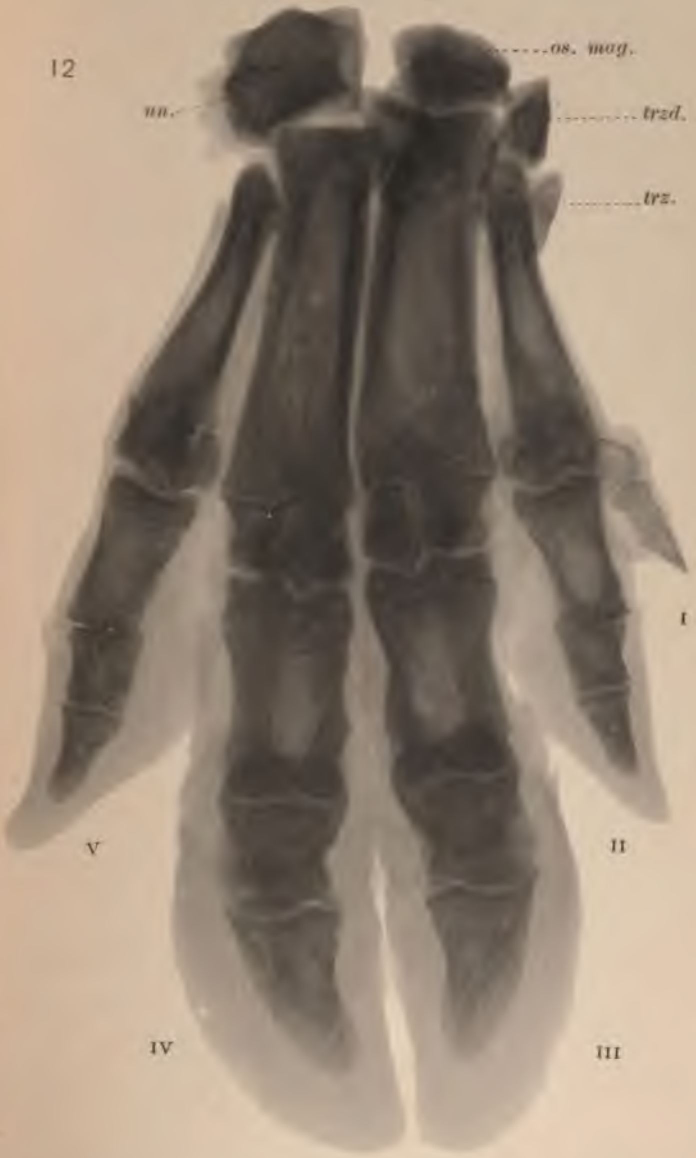

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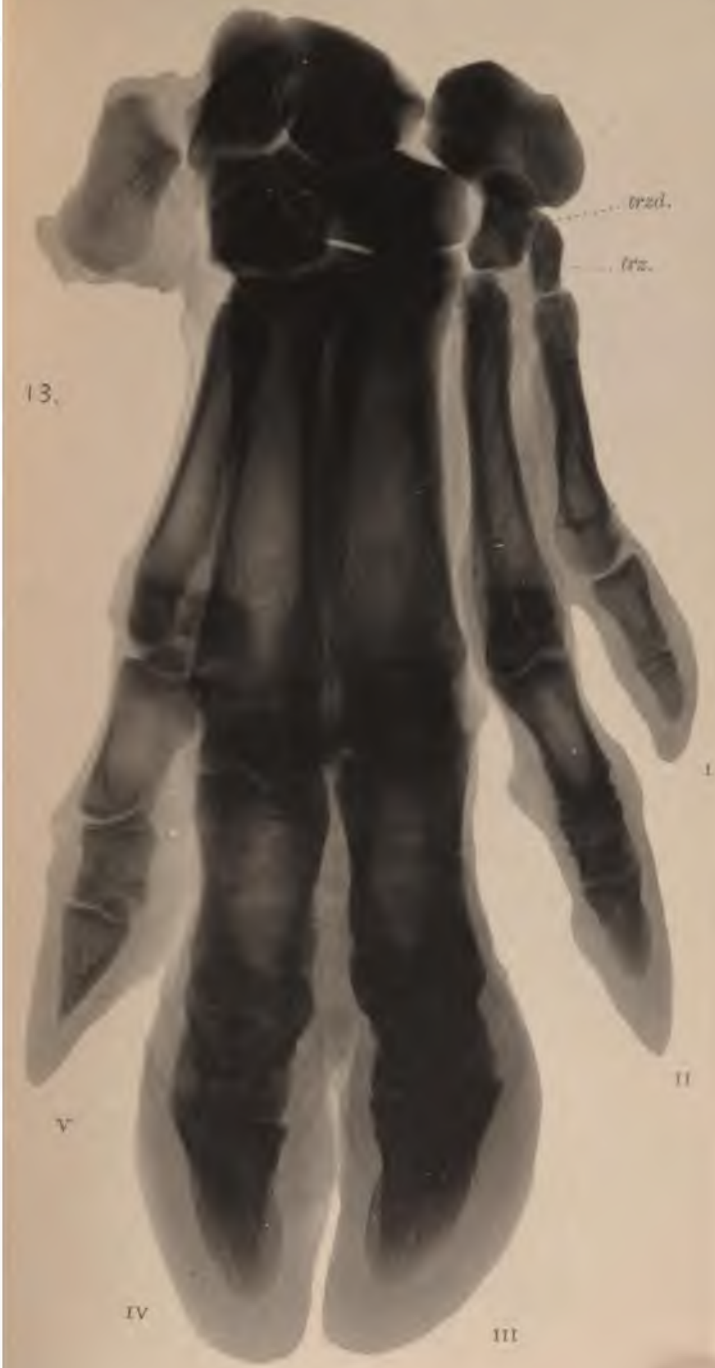
PLATE 5.

FIG. 13. Anterior view of the left polydactyle manus of the pig, showing a fully developed pollex (I) and the bones of the carpus.



13.

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PLATE 6.

FIG. 14. Anterior view of left polydactyle manus of the pig with one supernumerary digit (I), and digit II abnormally large.

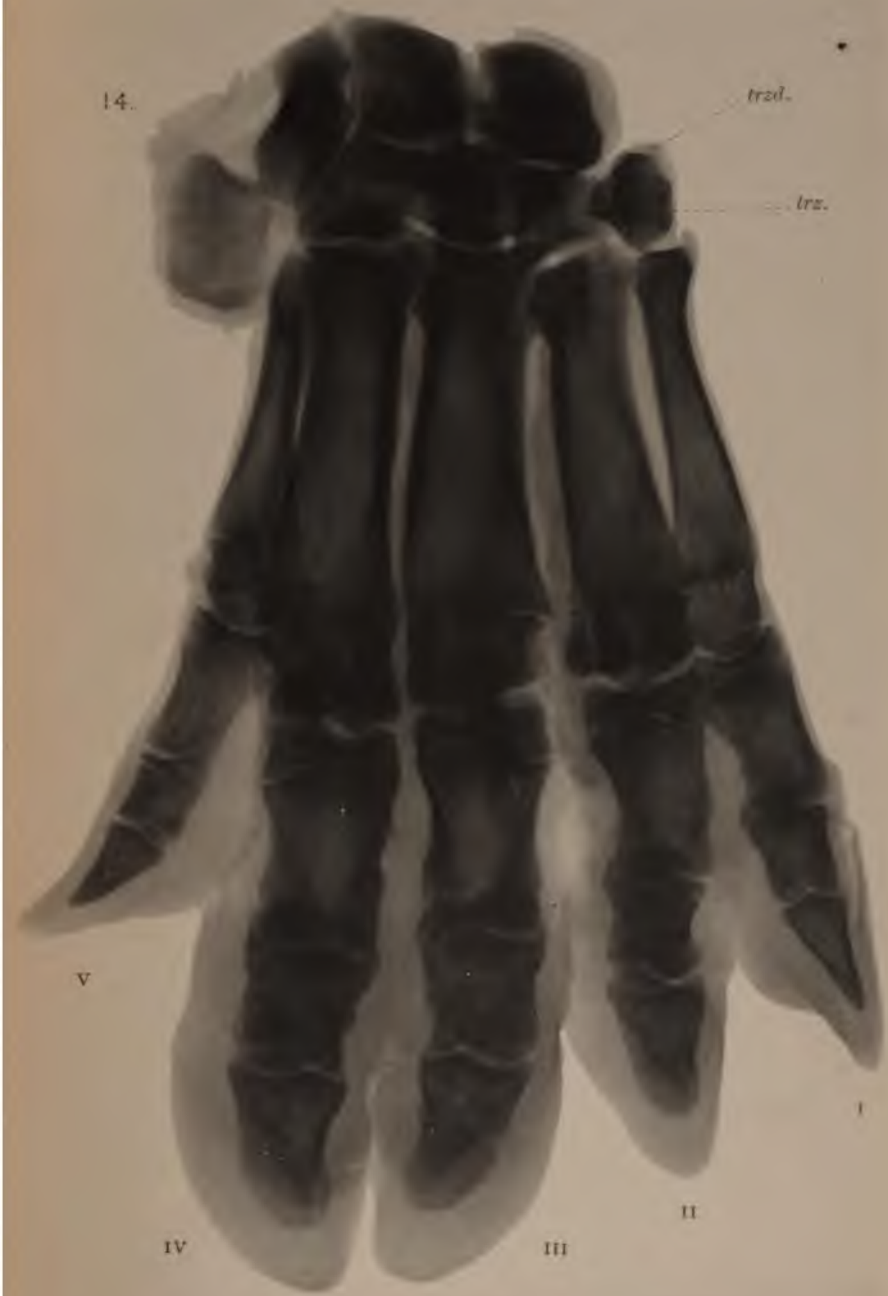

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PLATE 7.

FIG. 15. Anterior view of the left polydactyle manus of the pig, showing a supernumerary digit (I), to the proximal end of which the trapezium is fused.

15.

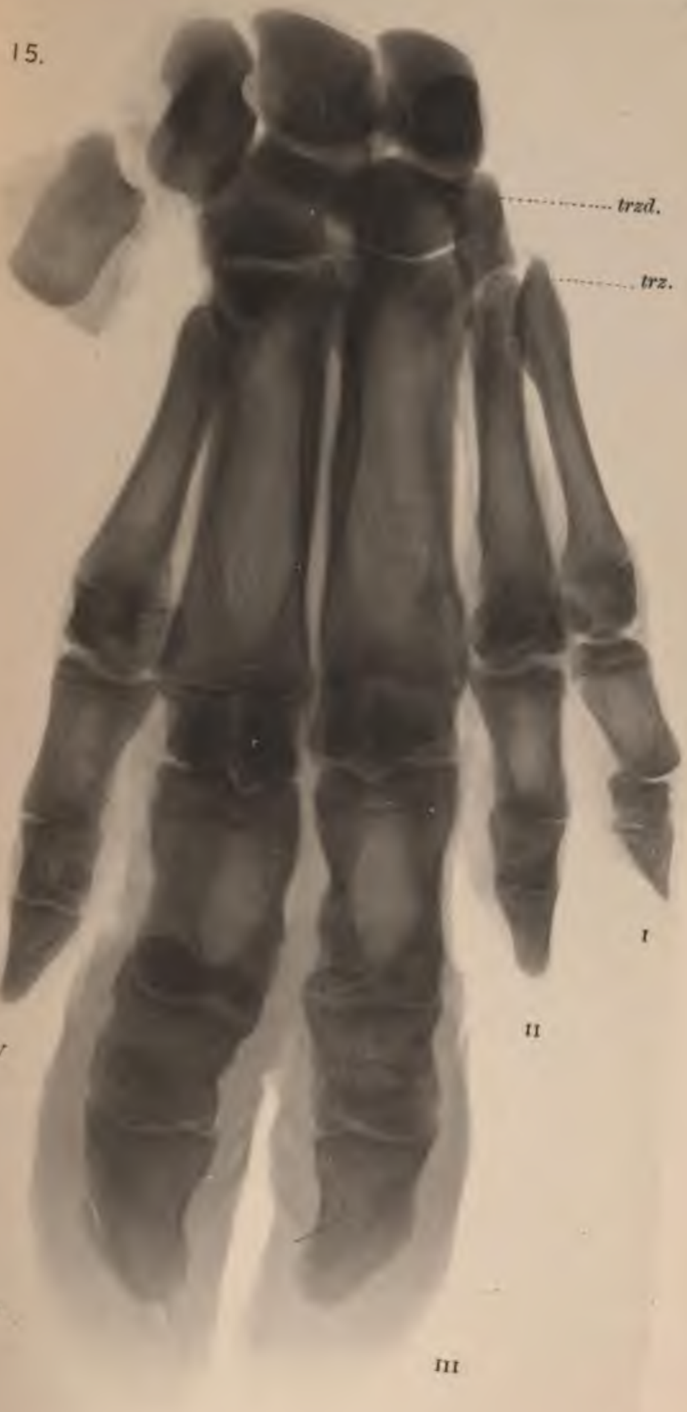

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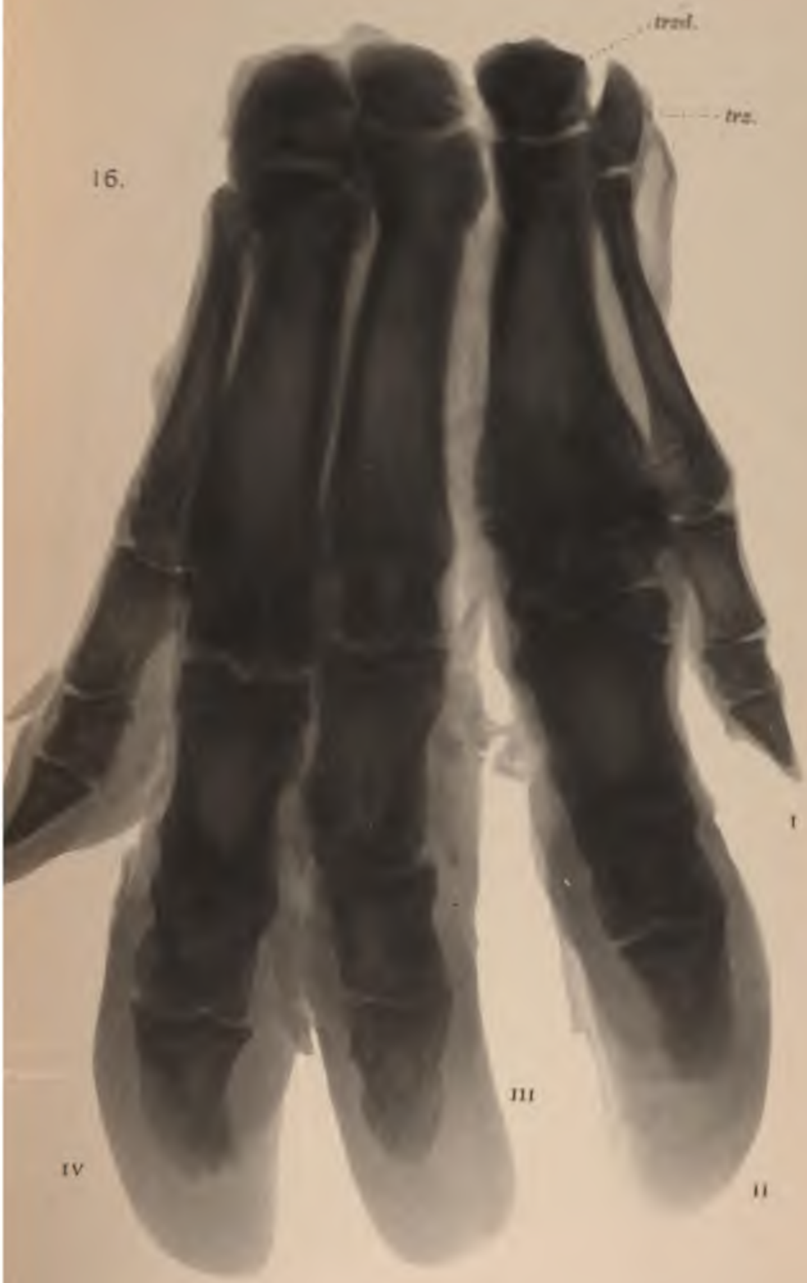
PLATE 8.

FIG. 16. Anterior view of the left manus of a polydactyle pig, showing the lower row of carpals, a supernumerary digit (I), and digit (II) abnormally developed.

PLATE 8.

16.



HELIOTYPE CO., BOSTON.

PLATE 9.

FIG. 17. Anterior view of the left manus of a polydactyle pig, showing the lower row of carpals and a large supernumerary digit (I).

17.

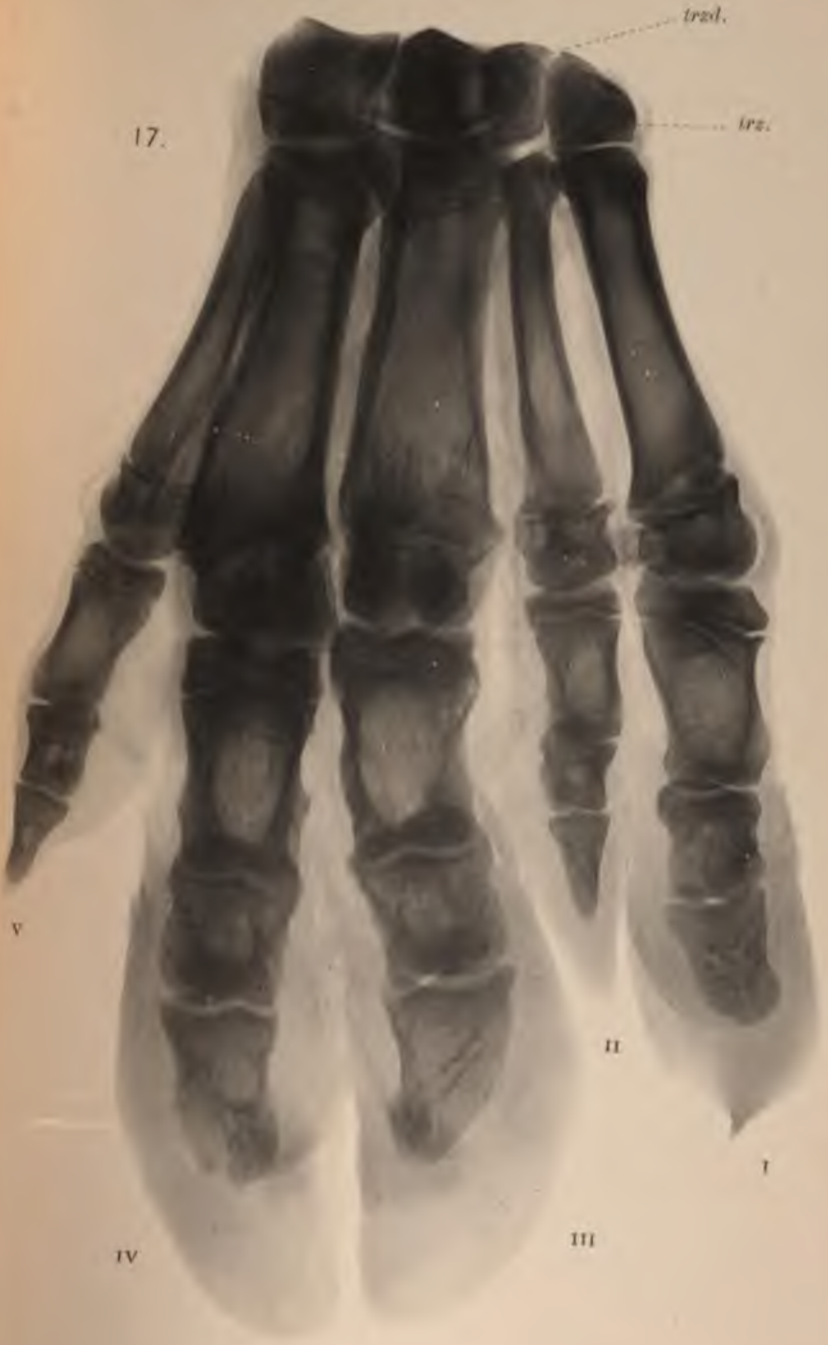


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PLATE 10.

FIG. 18. Anterior view of the right manus of a polydactyle pig, showing the lower row of carpals and two supernumerary digits borne on metacarpal I.

18.

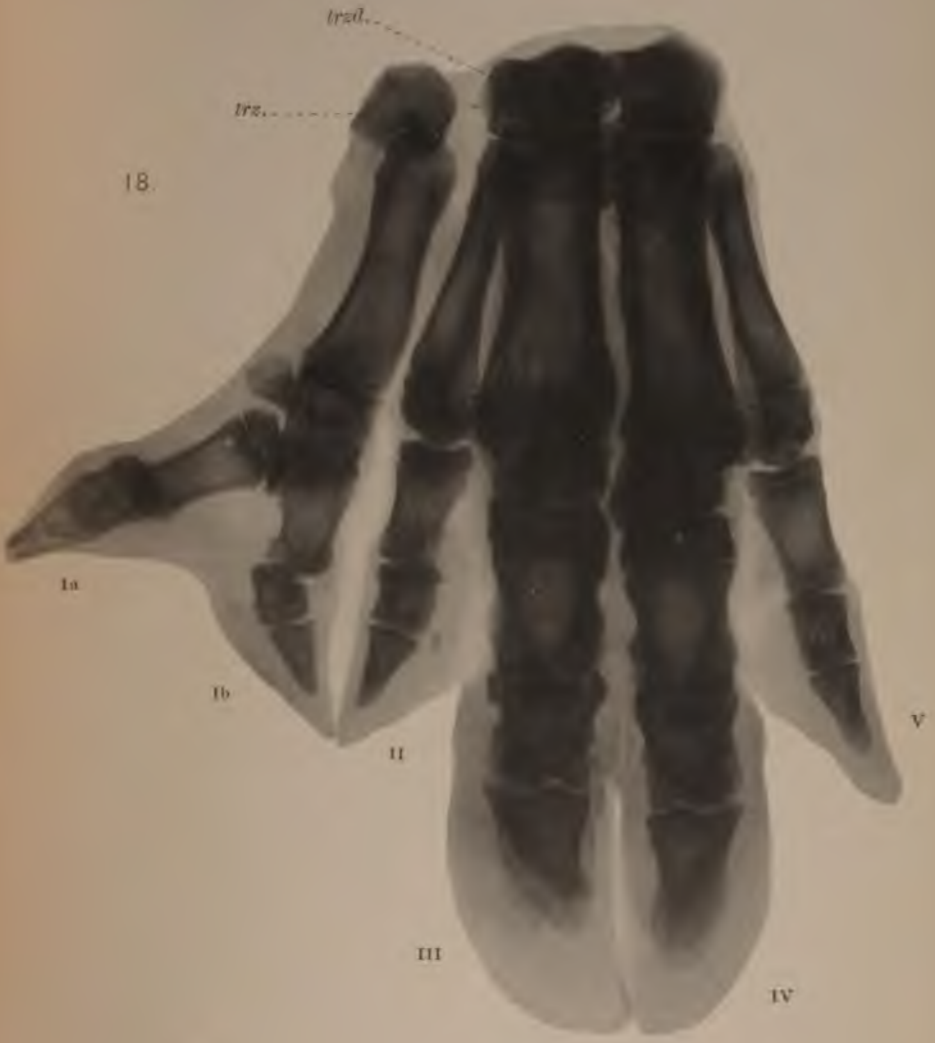

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PLATE 11.

FIG. 19. Anterior view of the left polydactyle manus of a polydactyle pig, showing the lower row of carpals, and two extra digits borne on metacarpal I.

19.

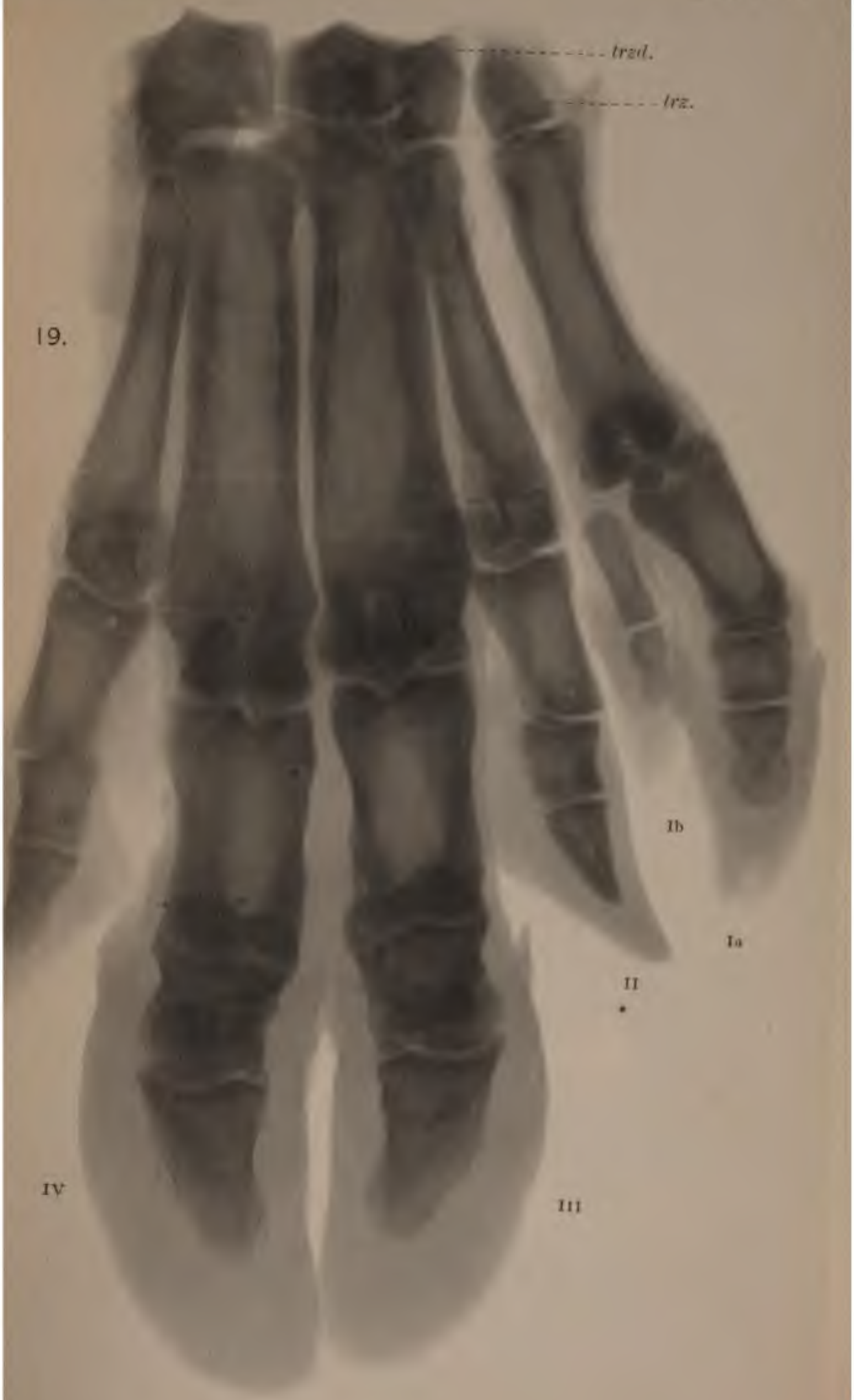

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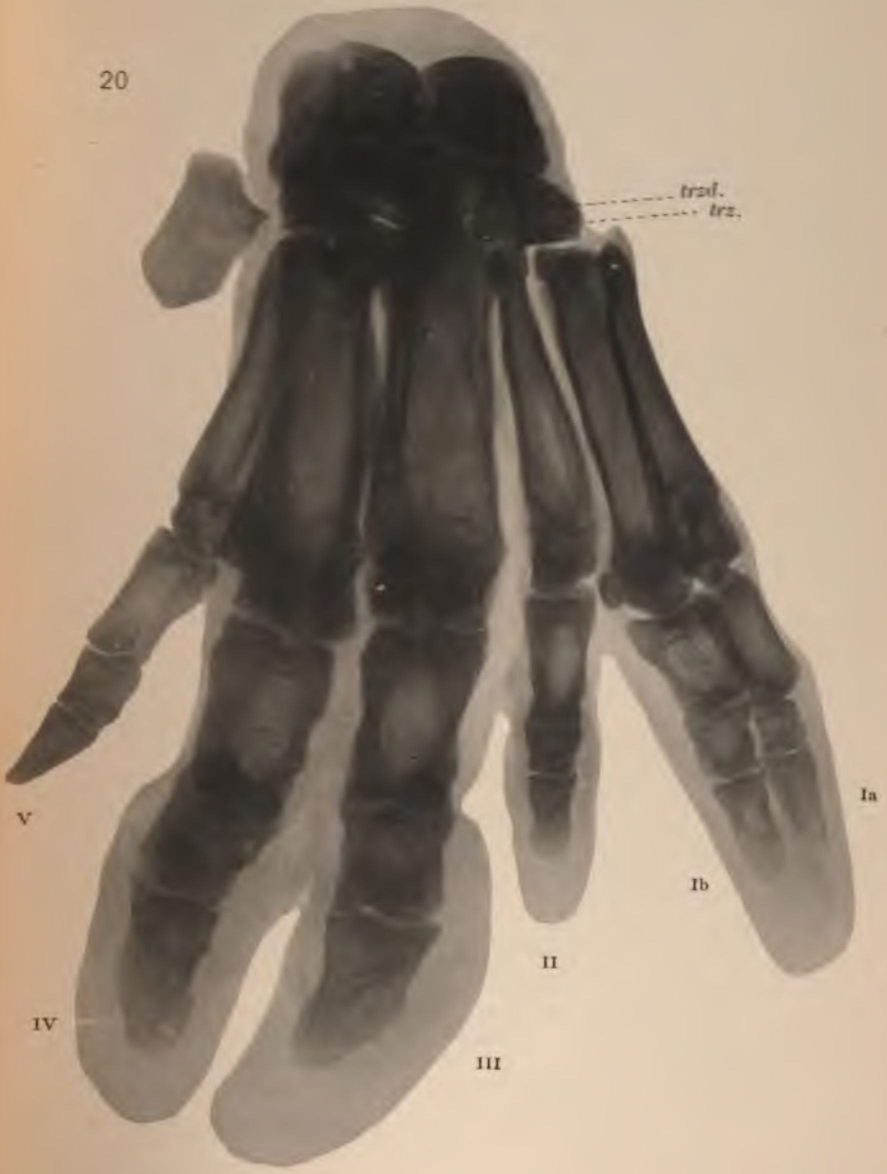
PLATE 12.

FIG. 20. Anterior view of the left manus of a polydactyle pig, showing two complete supernumerary digits enclosed distally in a single hoof.

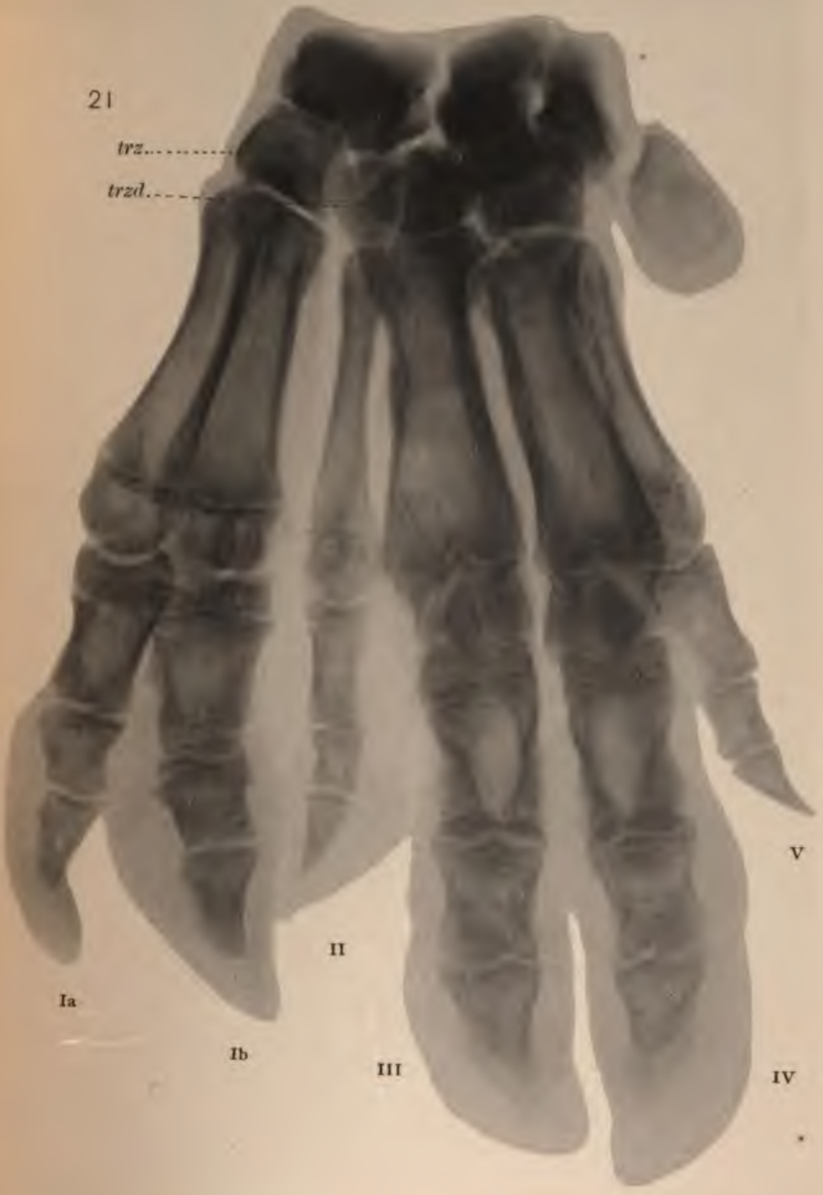
20



HELIOTYPE CO., BOSTON.

PLATE 13.

FIG. 21. Anterior view of the right manus of a polydactyle pig, showing two complete supernumerary digits.



HELIOTYPE CO., BOSTON.

-POLYDACTYLISM. PLATE 14.

2.

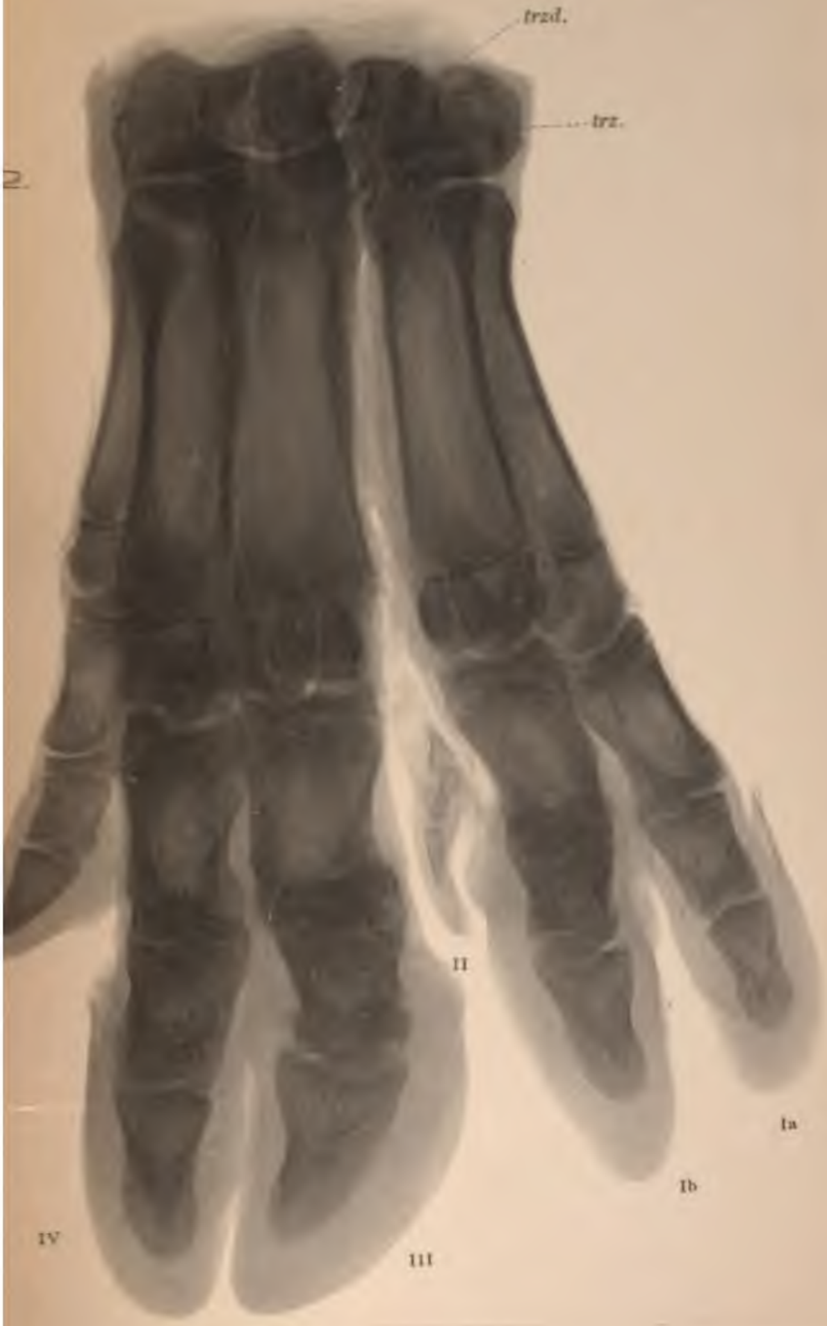


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PLATE 14.

FIG. 22. Anterior view of the left polydactyle manus of a polydactyle pig, showing the lower row of carpal bones, two supernumerary digits, and the rudimentary phalanges of digit II.

22.

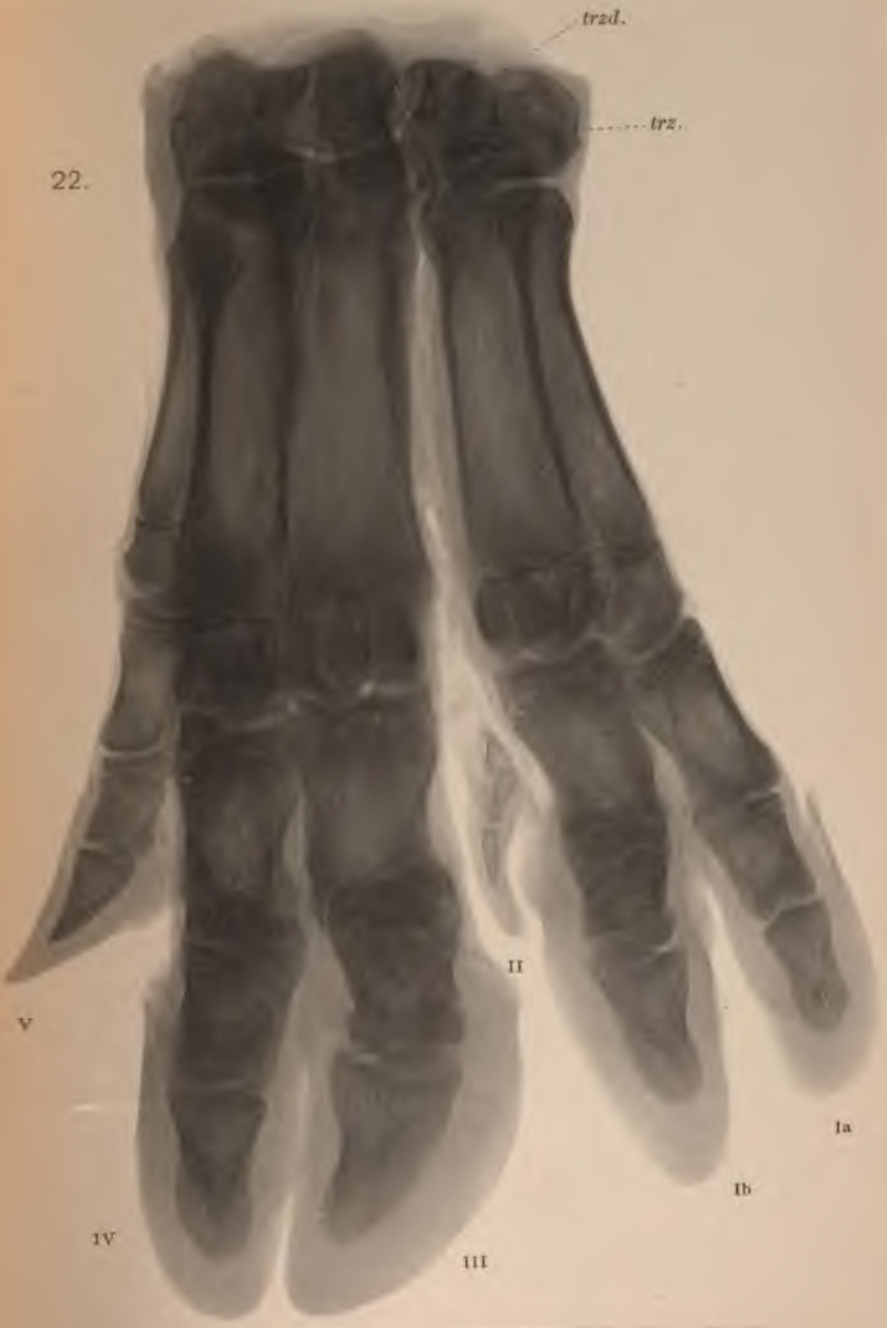

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PLATE 15.

Fig. 23. Anterior view of the left manus of a polydactyle pig in which two large supernumerary digits are present, but digit II is absent.

23.

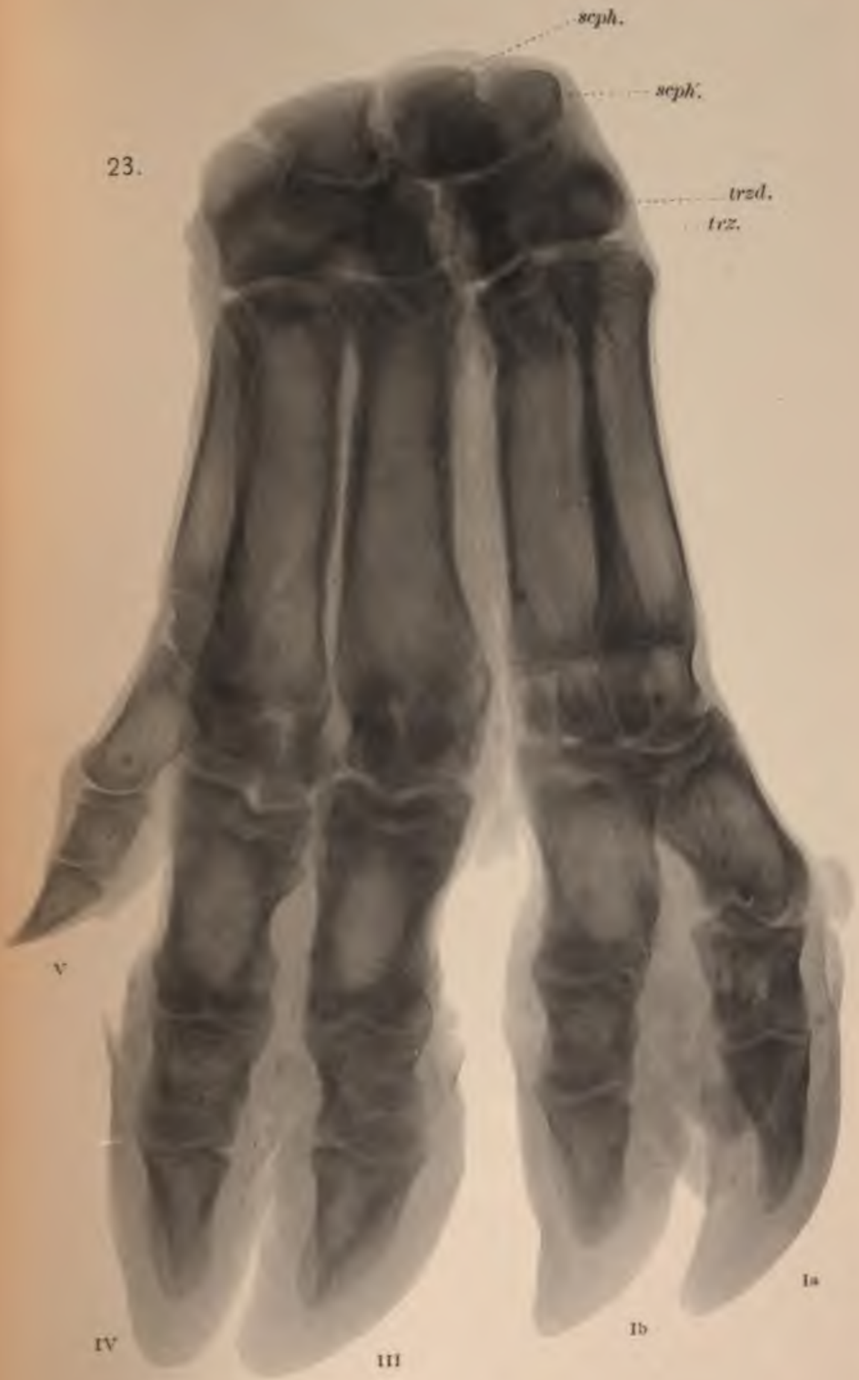

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PLATE 16.

Fig. 24. Anterior view of the left manus of a polydactyle pig, showing t[illegible] fully formed supernumerary digits, and the rudiments of a third.

24

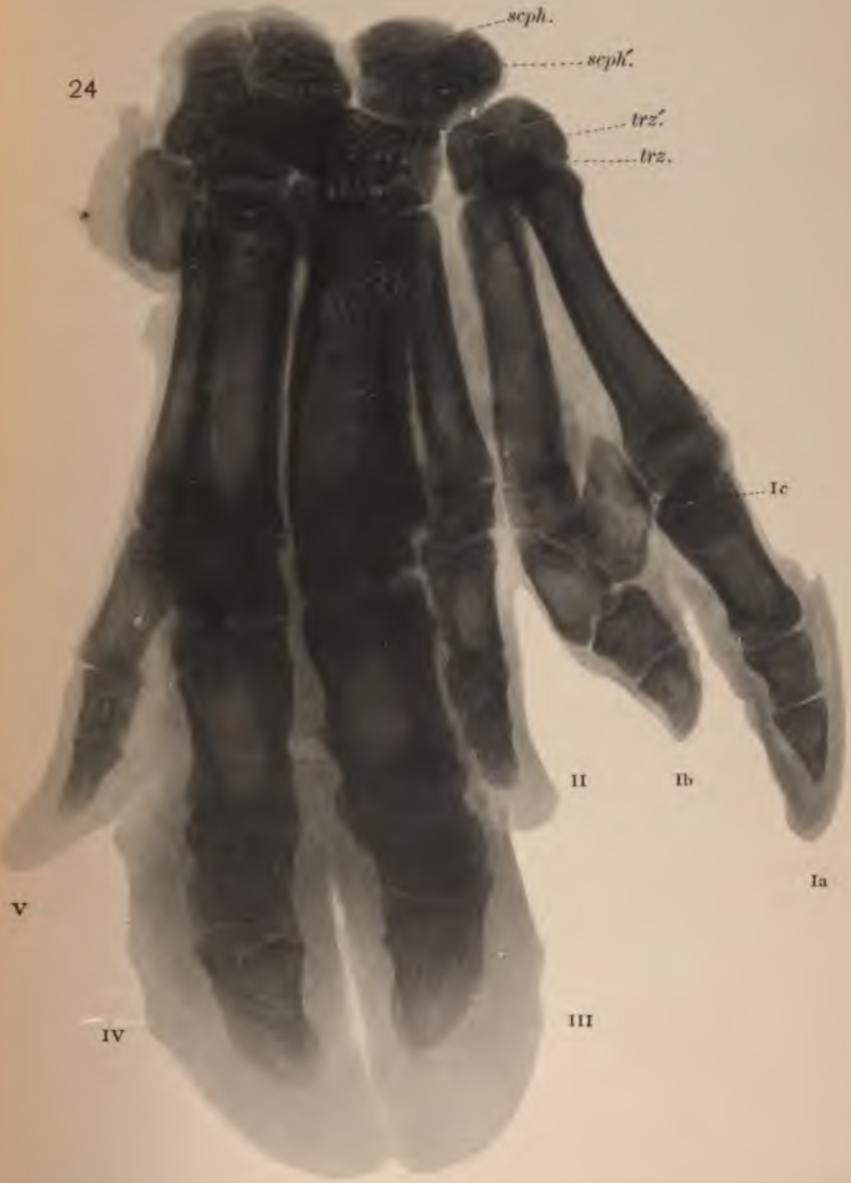

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PLATE 17.

FIG. 25. Anterior view of the right manus of a polydactyle pig, showing **an extr** digit borne on metacarpal II, and the lower row of **carpals**.

25.

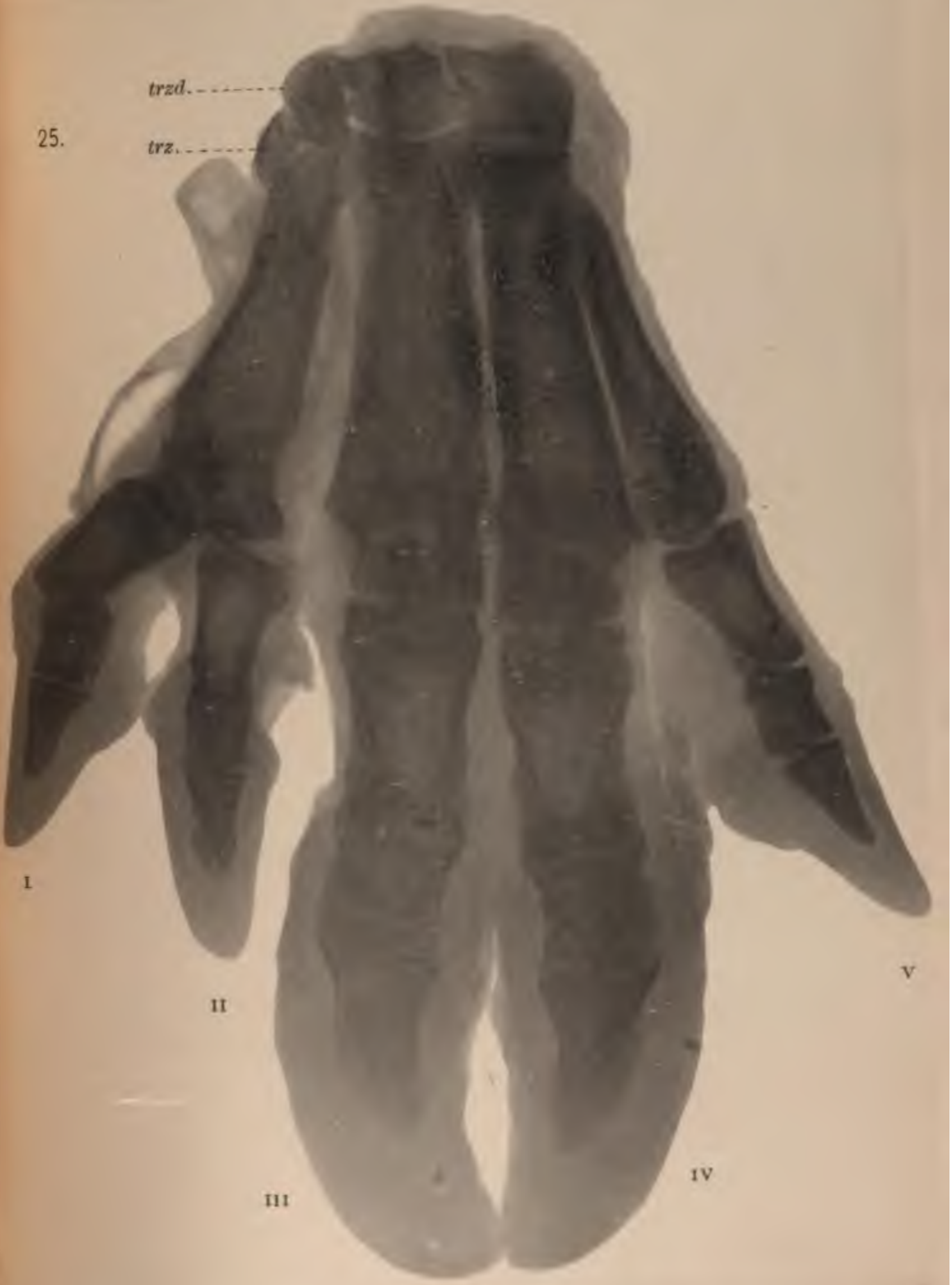

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PLATE 18.

FIG. 26. Anterior view of the left manus of a polydactyle pig, showing a large supernumerary digit, the metacarpal of which is fused to that of digit II.

26.

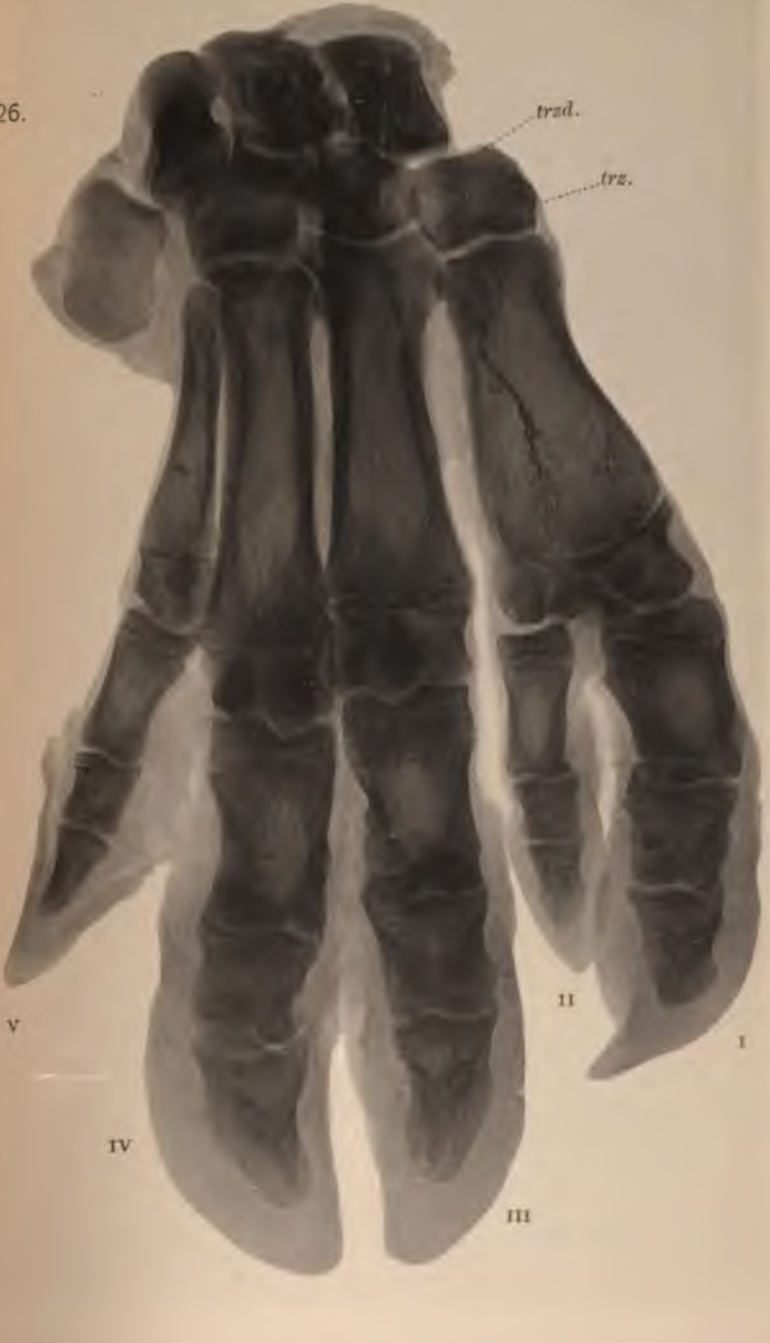

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PLATE 19.

FIG. 27. Anterior view of the left manus of a polydactyle pig, showing two extra digits, one of which is borne on metacarpal II.

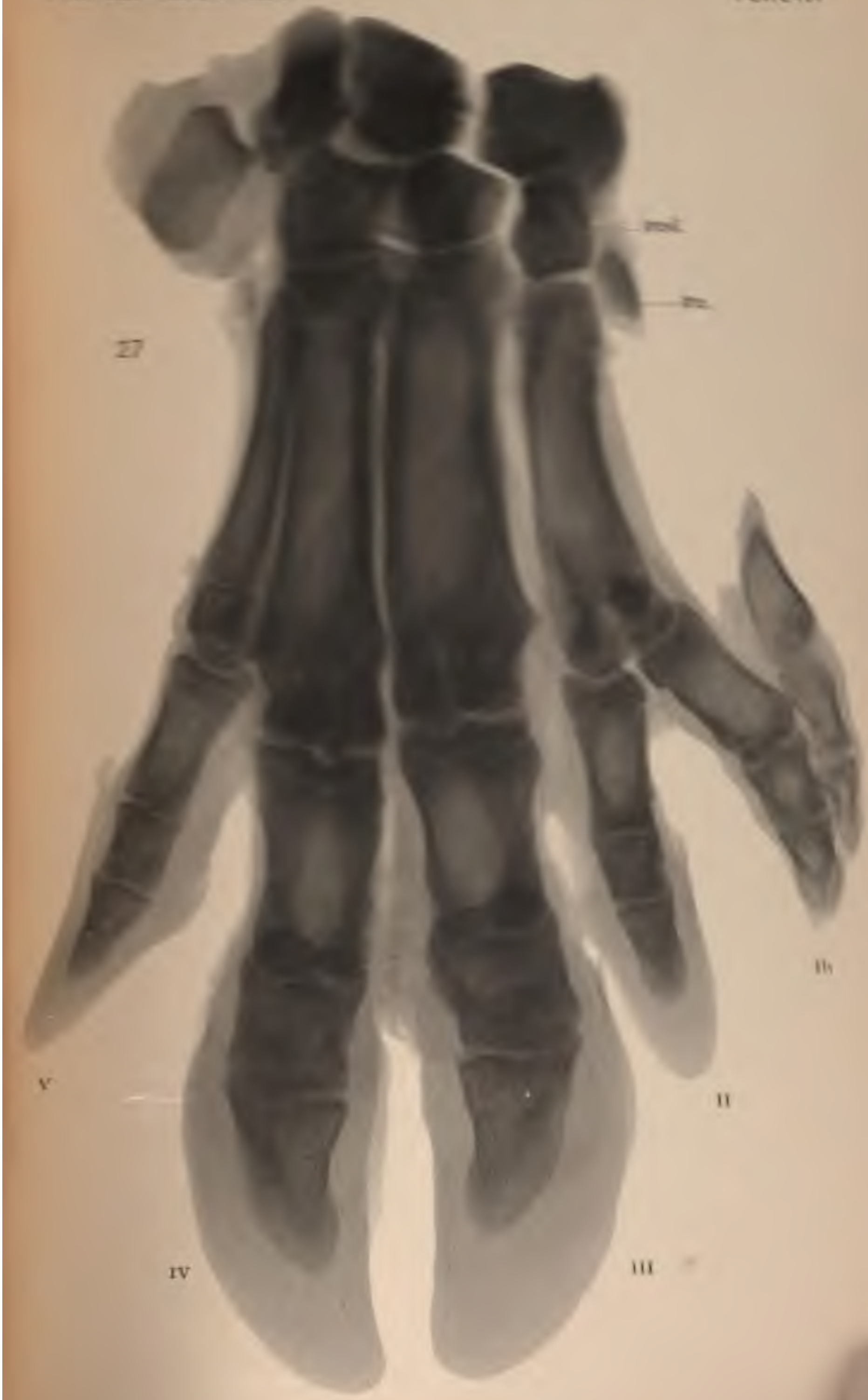

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PLATE 20.

FIG. 28. Anterior view of the left manus of a polydactyle pig, showing two extra digits, one of which (I^b) is borne on the same metacarpal with II.

28.

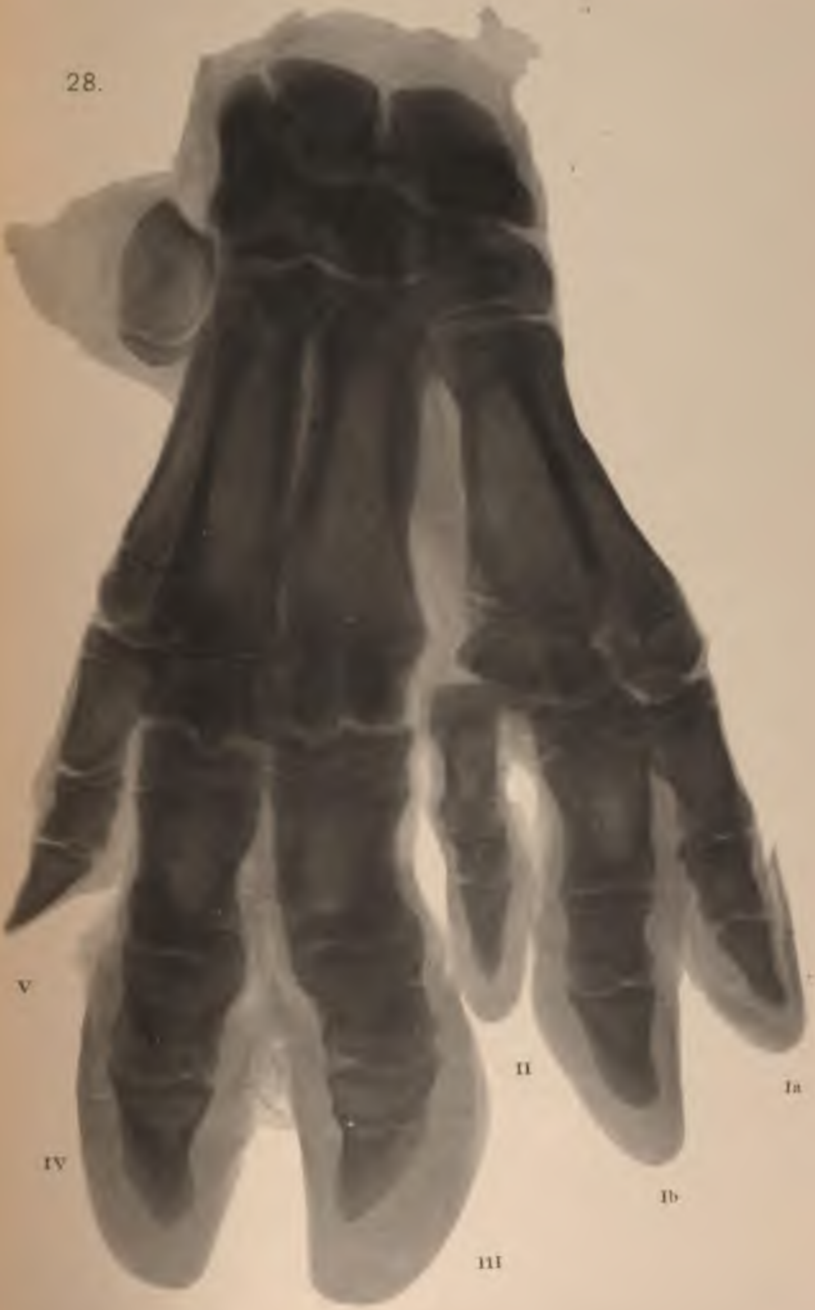

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PLATE 21.

FIG. 29. Anterior view of the left manus of a polydactyle calf, showing only the distal extremity of the metacarpus, and a supernumerary digit (II).

29.

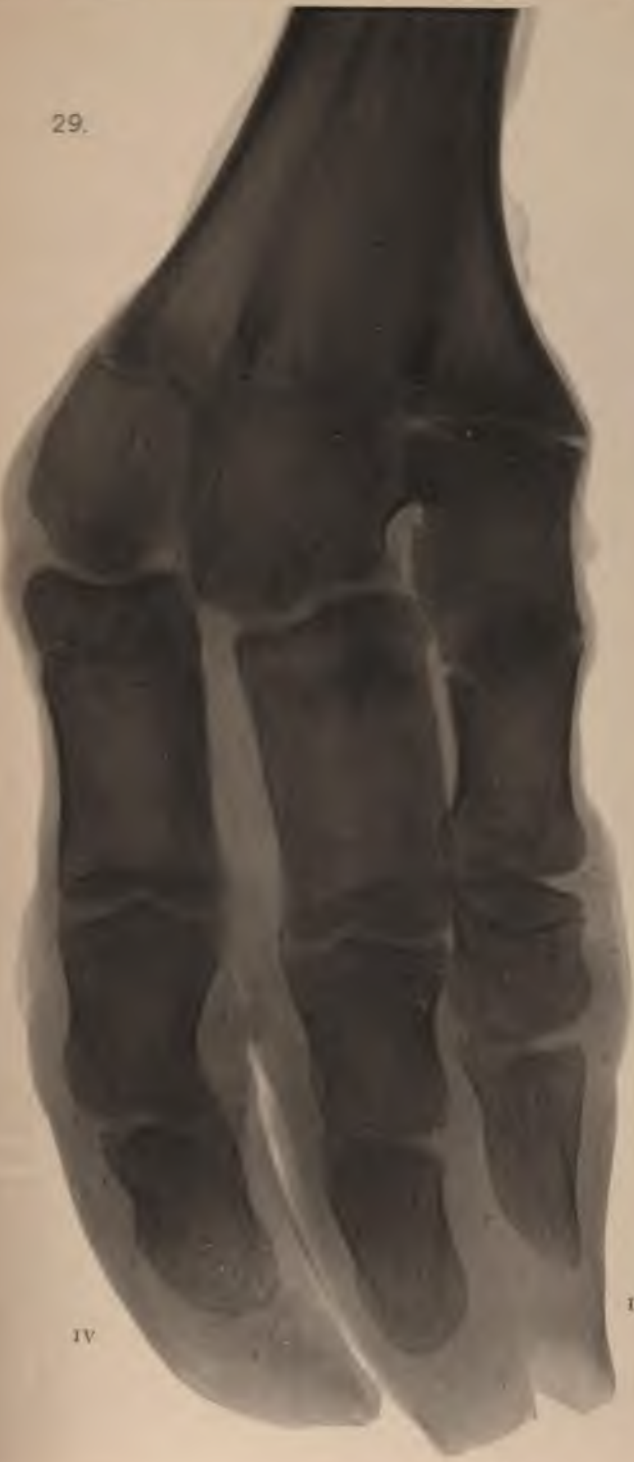

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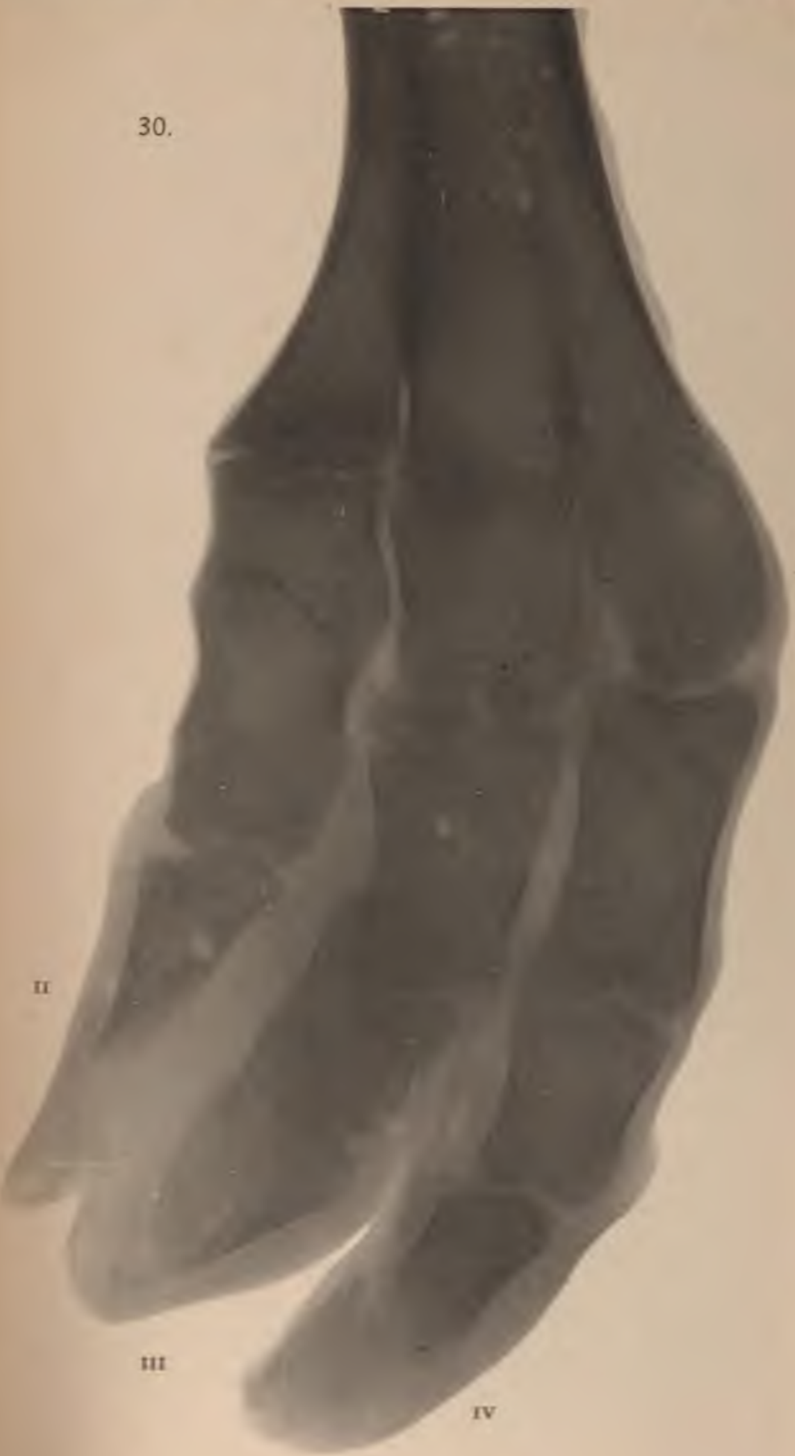
PLATE 22.

FIG. 30. Anterior view of right manus of same calf as Fig. 29, showing one extra digit (II).

30.



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E. L. Mark, *Director*.

⁂ Abbreviations used:—

B. M. C. Z. . . . . for Bull. Mus. Comp. Zoöl.
P. A. A. . . . . for Proceed. Amer. Acad. Arts and Sci.
P. B. S. N. H. . . . . for Proceed. Bost. Soc. Nat. Hist.

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12. Parker, G. H. — The Eyes in Scorpions. B. M. C. Z. **13**: 173–208. 4 pls. Dec., 1887.
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17. Parker, G. H. — The Histology and Development of the Eye in the Lobster. B. M. C. Z. **20**: 1–60. 4 pls. May, 1890.
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25. PARKER, G. H. — The Compound Eyes in Crustaceans. B. M. C. Z. **21**: 45–142. 10 pls. May, 1891.

26. WARD, H. B. — On some Points in the Anatomy and Histology of Sipunculus nudus, L. B. M. C. Z. **21**: 143–184. May, 1891.

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38. WOODWORTH, W. McM. — A Method of Orienting small Objects for the Microtome. B. M. C. Z. **25**: 45–47. Dec., 1893.

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40. DAVENPORT, C. B. — Studies, etc. — II. Regeneration in Obelia and its Bearing on Differentiation in the Germ-Plasma. Anat. Anz. **9**: 283–294. 6 figs. Feb. 15, 1894.

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43. WEYSSE, A. W. — On the Blastodermic Vesicle of Sus scrofa domesticus. P. A. A. **30**: 283–323. 4 pls. Dec., 1894.

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